COMPARATIVE STUDY OF TODIES (TODIDAE)

ARGIE KAY RIEFLER

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COMPARATIVE STUDY OF TODIES (TODIDAE): WITH EMPHASIS ON THE PUERTO RICAN TODY, *TODUS MEXICANUS*

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COMPARATIVE STUDY OF TODIES (TODIDAE): WITH EMPHASIS ON THE PUERTO RICAN TODY, *TODUS MEXICANUS*

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It is with particular pleasure I dedicate this book to an early student of todies, Alexander Wetmore, on the occasion of his 90th birthday.

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1
INTRODUCTION

As it sits on a twig in the verdure of spring, its grass-green coat is sometimes indistinguishable from the leaves in which it is embowered, itself looking like a leaf; but a little change in position, bringing its throat into the sun's rays, the light suddenly gleams as from a glowing coal. Occasionally, too, this crimson plumage is puffed out into a globose form, when its appearance is particularly beautiful.

Gosse (1847) on the Jamaican Tody

Objectives

This investigation, dealing with wild todies and concentrating on the Puerto Rican Tody (*Todus mexicanus*), is an attempt to document the natural history of the family Todidae, to determine the niches of each of the five species within widely differing communities, and to postulate the pathways of tody evolution. The information gathered is also relevant to basic zoological problems such as populations regulation in tropical birds, species abundance within tropical habitats, generalization and specialization of birds on oceanic islands, and ecological equivalency.

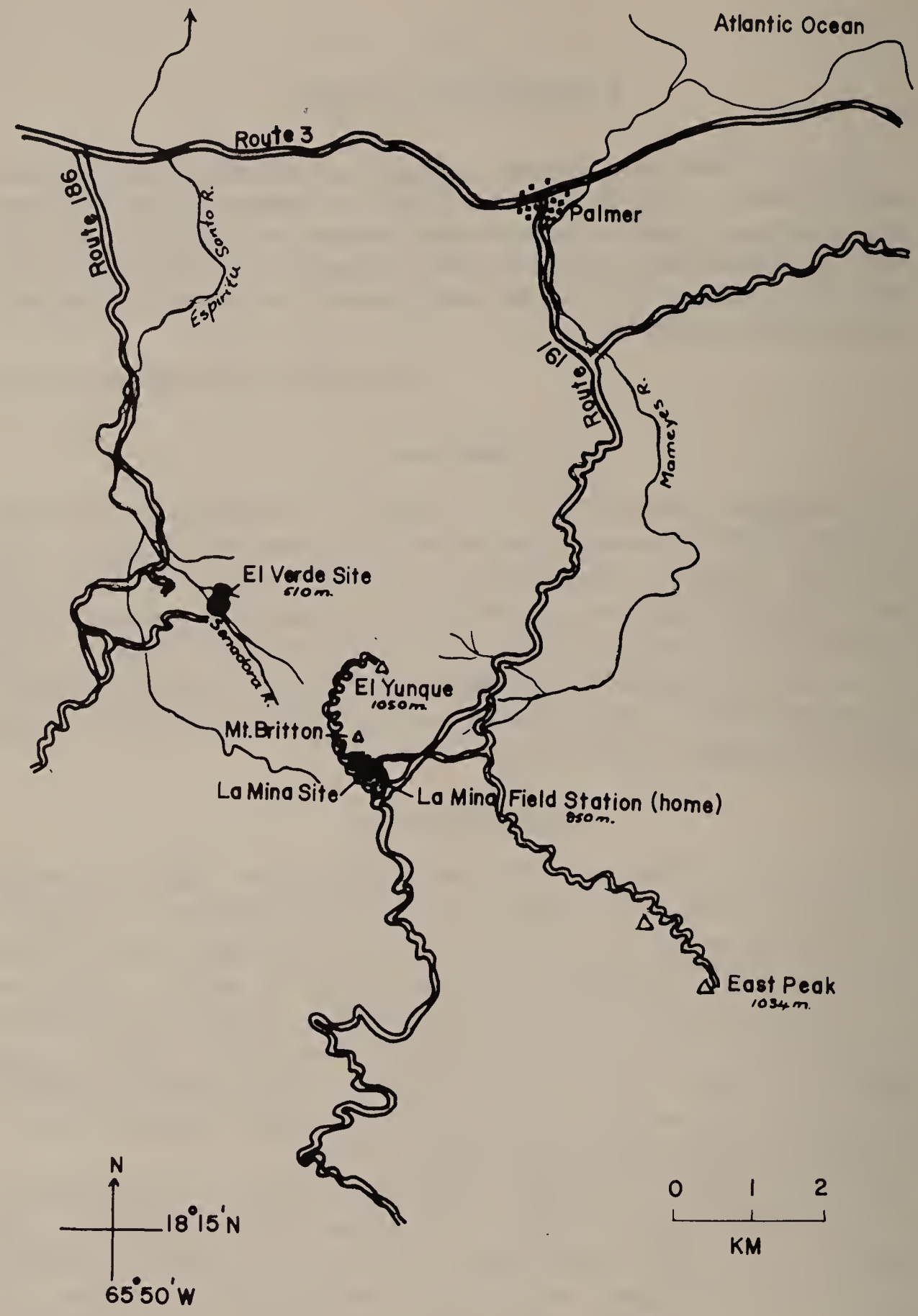
Study Localities

I lived in Puerto Rico for three years (September 1968 to November 1971), during which time I made a detailed investigation of the Puerto Rican Tody. This work was supplemented by trips throughout the Caribbean and parts of South America in order to study other species of *Todus* and birds of related interest, such as tody–flycatchers, motmots, and jacamars. Over 2,000 hours were spent gathering data in Puerto Rico, where I engaged in field work almost every day for the first two years (1968 to 1970); in the final year work was less concentrated and major trips were taken to other Greater Antillean and Puerto Rican islands.

Our isolated house was ideally suited for this study. It was located at the La Mina Field Station, roughly in the center of the 11,200 ha Luquillo National Forest in eastern Puerto Rico, at an elevation of 800 m and situated among transitional ridgetop vegetation. From this base I worked at all elevations in the rainforest, concentrating population studies within two study sites (Map 1.1; Appendix 2).

La Mina–Mt. Britton Site, Puerto Rico

This triangular area (Fig. 1.1) of approximately 35 ha is situated on the southeastern slope of El Yunque from an altitude of 800 to 1,000 m and is bounded on two sides by roads, the Mt. Britton trail completing the isosceles. A trail runs centrally from the lower corner to join the base of



MAP 1.1 El Yunque, Puerto Rico, showing access roads, rivers and two principal study areas.

the triangle, allowing me easy access to the steep, matted ridges on the El Yunque Road side.

The dominant vegetation is Sierra Palm forest grading into transitional, ridgetop, and elfin forests. The characteristics of these vegetation types

FIG. 1.1 La Mina Field Station from East Peak Road. Behind it, radiating in an isosceles triangle, lies the study area. Three vegetation zones are apparent: Elfin Forest along highest ridges, Sierra Palm belt (pale areas) and Colorado, mixed with transitional forest.

are described fully in Chapter 2. Although not purely virgin, the forests here have been little disturbed.

The presence of four houses within the forest had little effect on tody distribution; in fact, two pairs of todies included the La Mina Field Station within their territories.

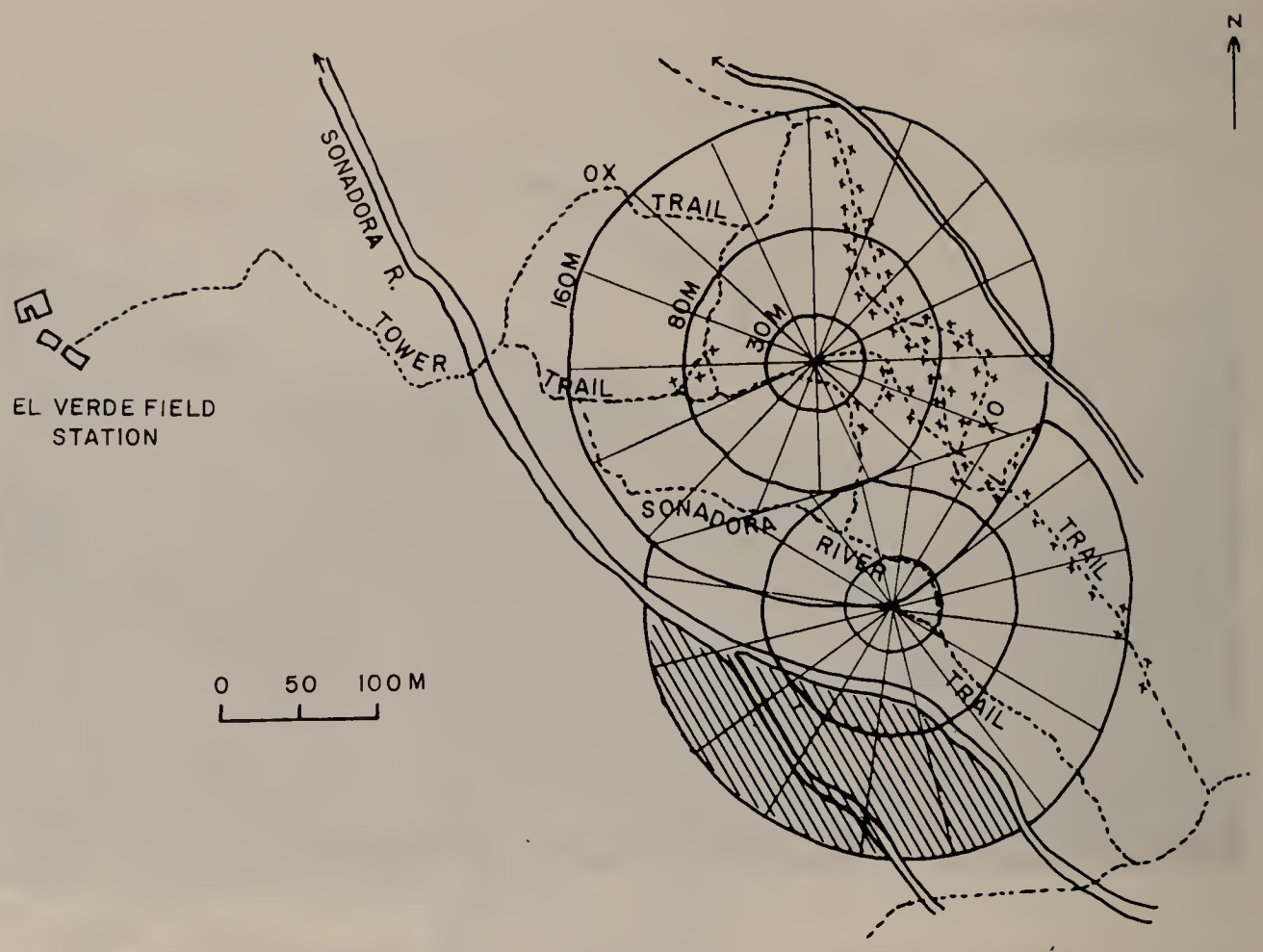
EL VERDE SITE, PUERTO RICO

This 10 ha area (Map 1.2), shaped like two, partly overlapping, circles is at 424 m on the northwestern slope of El Yunque. It forms part of the Espíritu Santo drainage basin and includes its large, boulder-strewn tributary, the Sonodora River. The river flows through the southwest corner, and one of its tributaries flows through the northeast.

The vegetation consisted mainly of "Tabonuco" forest with some "Colorado" forest. This area has been periodically lumbered since the 19th century and no virgin forest remains.

OTHER SITES IN PUERTO RICO

Every three months I worked temporarily in different island habitats (Map 1.3), always including the Guánica region, which is a lowland dry limestone forest, as well as at localities in wet limestone karst country



MAP 1.2 El Verde, Puerto Rico, showing rivers, trails, and tody nesting banks (marked by X's; each X does not correspond to one nest, but merely indicates possible banks). Owing to difficult terrain and accessibility, I covered only 8.4 of the 10 ha; shading indicates the unstudied portion.

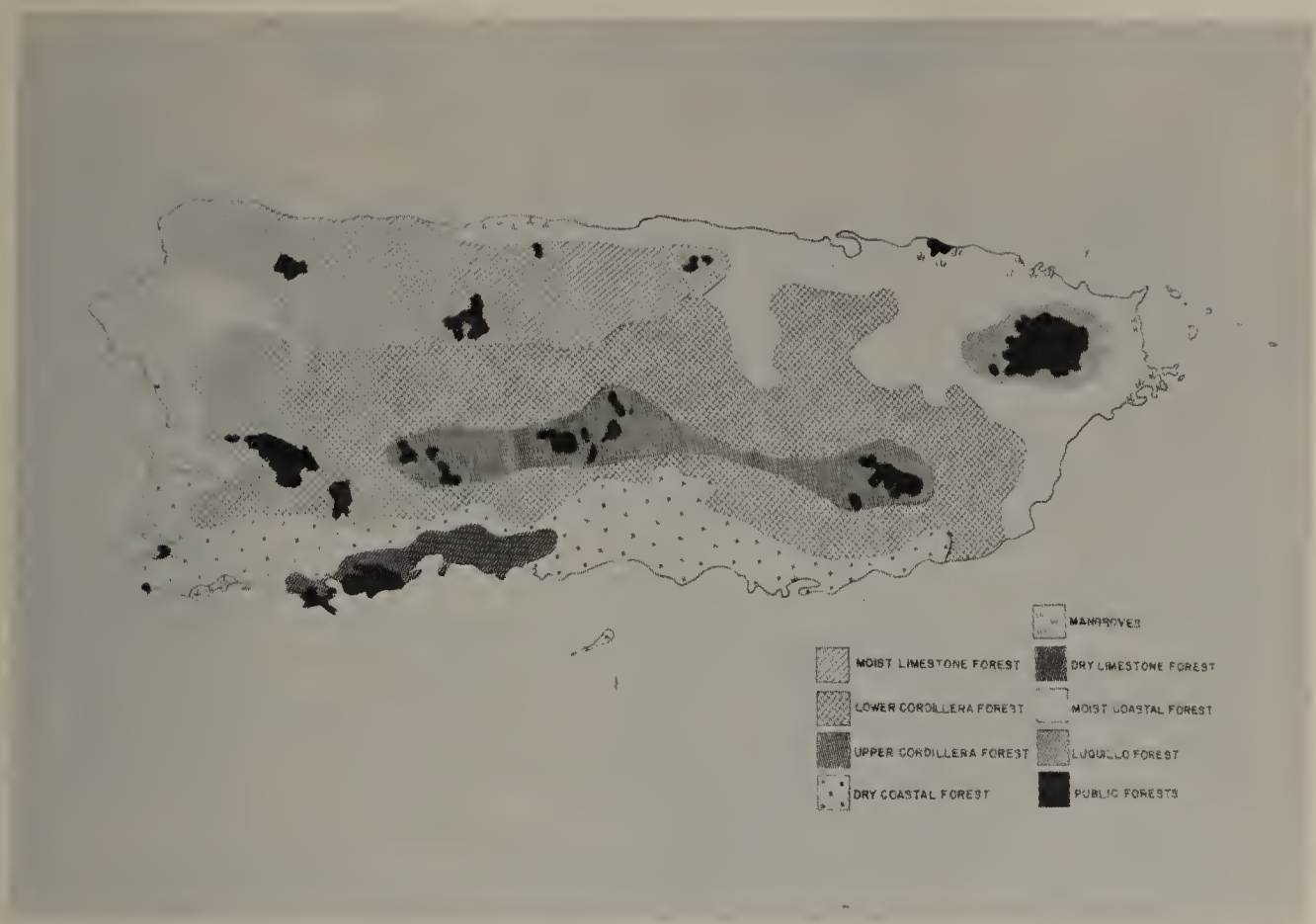
(Guajataca, Río Abajo), high montane forest (Carite–Guavate, Toro Negro, Guilarte), low montane forest (Susua, Maricao), or coffee plantations or "*cafetales*" (Aibonito, Cidra). I also checked habitats in second-growth of various stages, marginal riparian fields, pastures, and other much disturbed areas, including housing developments, dry and wet coastal forests, and mangroves (brackish, fresh water, or marine "hammocks" surrounded by coral reefs). These covered all of Puerto Rico's habitat types, all elevations from sealevel to the highest peak (Cerro de Punta, 1,463 m), and representative rainfall belts from 750 to over 5,000 mm/year. Each major habitat will be further discussed in relation to tody population densities (Chap. 2).

Only 0.4% of Puerto Rico's land remains virgin; even most of the once forested Cordillera Central is now grass or scrub (Fig. 1.2). As a consequence todies can be studied profitably only in forest reserves.

We searched for todies on 24 islands and several reef-enclosed hammocks that ranged offshore from 50 m to 60 km.

OTHER GREATER ANTILLEAN ISLANDS (Appendix 1)

I studied the Cuban Tody (*T. multicolor*) for one week at Guantanamo Naval Base in arid southeastern Cuba (August–September 1971) and observed



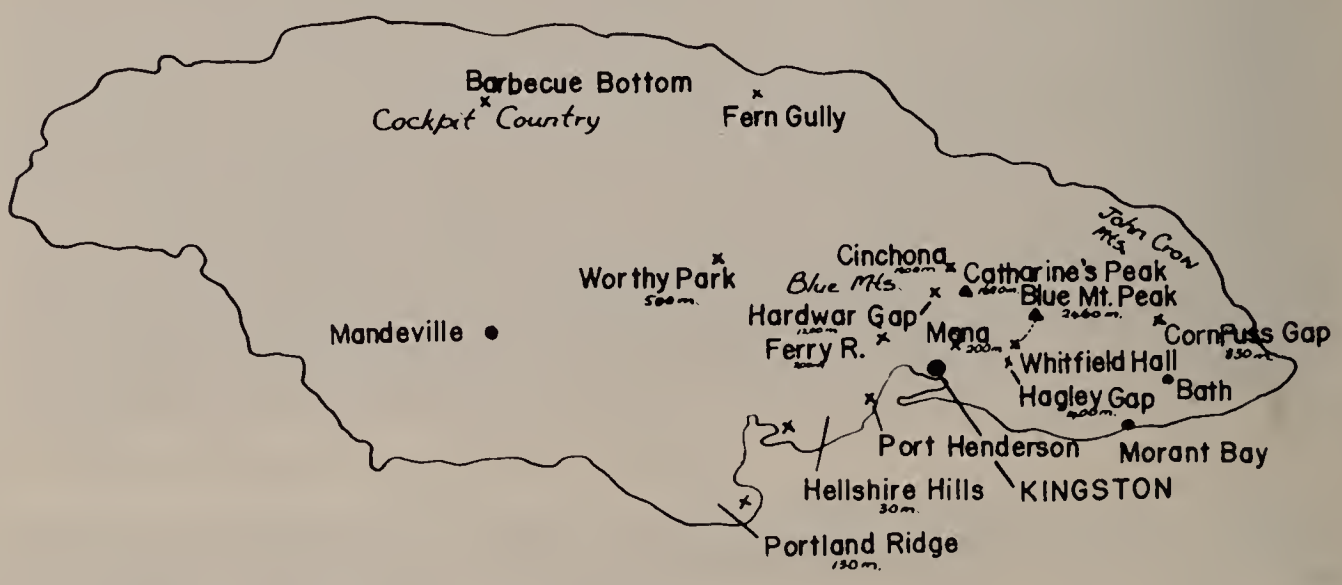
Map 1.3 Top. Vegetation of Puerto Rico.

Bottom. Distribution of *T. mexicanus* in Puerto Rico. Based on this study, Raffaele (pers. comm.), and Wetmore (1916). Dotted lines are approximate boundaries. All other areas (except public forests) are partly or totally cleared, supporting todies only in patches of scrub or second-growth.

FIG. 1.2 Typical view of the deforested Cordillera Central, Puerto Rico (near Aibonito, 1969).

the Jamaican Tody (*T. todus*) for 17 days (January 1969; April–May, 1971) in habitats ranging from sealevel to rainforest at 1,800 m (Map 1.4).

Three days in Haiti (February 1969) made possible limited study of the Broad-billed Tody (*T. subulatus*) in coastal arid scrub and up to 900 m



MAP 1.4 Primary study areas in Jamaica. Crosses indicate census locations.

on the Massif de la Selle. Twelve days in the Dominican Republic (March–April 1971) were more productive, owing to considerably less habitat destruction, and I could study Broad-billed and Narrow-billed (*T. angustirostris*) Todies both in allopatry and sympatry. I spent all my time in the south, covering the lowlands and mountains west of Santo Domingo from sealevel to 2,100 m in the Baoruco Range adjacent to Haiti and to 1,150 m in the Cordillera Central.

Methods

Norelco and Uher portable casette tape recorders, 8 × 40 binoculars, a waterproof diving watch, and a notebook were my chief tools. I used no blinds, yet todies occasionally came to within one meter of me. Their tameness and tolerance of humans were such that, as long as I remained at a reasonable distance, I had no need to conceal myself completely.

For investigating burrow chambers I used a "Conductalite" (National Camera Ltd.), a modified penlight which transmits light from a bulb through a piece of plastic tubing. The light, emerging at the far end onto a slanted adjustable small mirror was then transmitted farther down the tunnel at an angle to its original path. In most cases the nesting chamber was then visible.

Mistnets posed many problems, chiefly because todies detected their presence. Barlow, Diamond, Dick, and Lack, (pers. comm.) also reported this difficulty. Therefore, my husband and I designed a small net that proved ideal for capturing adults within burrows. We sewed an "invisible" (1.3 cm mesh), nonelastic ladies' hairnet around a wire coat hanger that had been made into a circle about 20 cm in diameter (todies flew straight through unstretched 2 cm mesh) and attached this by nylon cord to a bamboo pole four meters long.

Attempts to catch todies outside their burrows were largely unsuccessful, so I tried to minimize nest desertion by capturing adults only after the sixth day of the nestling period, by which time the young could also be banded and the adults were less wary.

Todies have extremely slender tarsi (1 mm in diameter); the most successful bands were cut-down, colored, plastic British ones (A. H. Hughes and Co.).

Using "Aeroxon" sticky flypaper traps (72.5 cm long; active ingredients resin, rubber, and mineral oil), my husband and I took monthly measurements of insect density at 20 stations in both the Luquillo and Guánica Forests. Each station represents a different vegetation zone or subhabitat. We recorded numbers, sizes, and orders of insects captured, giving us a simple assay of relative insect densitites, seasonal variation, and a comparison of the two forests.

We conducted one-kilometer strip censuses during early mornings along previously surveyed trails. All todies seen or heard were recorded and the positions of one or both members of the pair was noted. Through experience I estimate that todies can be heard up to 50 m from the observer in all habitats. Censusing was systematic throughout the year in Puerto Rico and

opportunistic elsewhere. A linear census technique was used due to the difficult terrain, which was often steep and inpenetrable, especially in wet forests.

Measurements were made with a plastic ruler, sometimes in combination with flexible roots or sticks. Photographs were taken with Pentax and Canonflex cameras, using color and black–and–white film. A standard United States Weather Bureau gauge measured rainfall. The United States Forest Service supplied colored marking tape and surveying equipment for determining territory sizes and for marking nests. I used large "Havahart" live traps and rat traps for capturing mongooses; the latter, which were attached to trees by wire and arranged in several sets of three-meter trap lines, proved unsuitable.

Previous Studies

Few ornithologists have studied todies, despite their tameness and abundance in a variety of habitats. The natural history of the family has been documented only superficially. Wetmore (1916, 1927) and Wetmore and Swales (1931), the basic references, give information on stomach contents of birds collected and brief notes on behavior and ecology. Other authors that have made passing reference to feeding or nesting habits of todies are Attewell (1907), Barbour (1943, 1945), Bond (1949, 1956, 1961), Christy (1897), Danforth (1929, 1931, 1935), Daniel (1902), Gosse (1847), Jeffrey-Smith (1956), Recher (1965, 1966, 1970), Rolle (1960, 1963), Smith (1970), and Salmon (1969, 1971). Virtually no quantitative information exists except for population estimates of *T. mexicanus* in two study plots within Luquillo forest (Recher, 1965).

Morphology

The five species—one each on Cuba, Jamaica, and Puerto Rico and two on Hispaniola—in the family's single genus, *Todus*, are morphologically very

TABLE 1.1

KEY TO THE SPECIES OF *Todus*

1A. Flanks yellow; no pink ..... *T. mexicanus* (Puerto Rican Tody)

1B. Flanks with pink

  2A. Blue subauricular patch

    3A. Yellow lores, much pink on flanks, whitish belly ..... *T. multicolor* (Cuban Tody)

    3B. No yellow lores, little pink on flanks, yellow-green belly ..... *T. todus* (Jamaican Tody)

  2B. No blue subauricular patch

    4A. Broad bill, no black on mandible, yellowish belly ..... *T. subulatus* (Broad-billed Tody)

    4B. Narrow bill with mandible distally black, whitish belly ..... *T. angustirostris* (Narrow-billed Tody)

TABLE 1.2

MEASUREMENTS

	multicolor	*todus*	*angustirostris*	*subulatus*	*mexicanus*
Number of specimens	82	27	26	83	104
Wing Chord (mm)	43.8	46.0	46.0	50.3	42.8
Bill Length (mm) [1]	12.3	13.9	12.6	14.3	13.3
Bill Width (mm) [2]	4.3	4.4	3.9	5.4	4.4
Weight (gr)	-	6.4 [3]	-	-	5.4 [4]

1) From distal edge of nostril
2) At distal edge of nostril
3) Twelve specimens
4) Three specimens

similar. All are shining green above, with pale underparts, a prominent red gorget, stout bodies, and long, flat, red bills. Differences in flank color (pink or yellow), the presence or absence of a small blue subauricular patch, and vocalizations distinguish the five species (Table 1.1).

The Puerto Rican Tody (*T. mexicanus*) can be distinguished by the absence of pink on the flanks; other species always show some pink intermingling with the characteristic yellow or yellow-green of this area. The Cuban Tody (*T. multicolor*) has sky-blue subauricular feathers, while in the Jamaican Tody (*T. todus*) these are blue-gray. The remaining two taxa, the Narrow–billed (*T. angustirostris*) and Broad–billed (*T. subulatus*) Todies, are extremely similar, having only slight variations in dorsal and ventral hue and in bill width. In general the latter is bigger (Table 1.2) with more iridescent green on the back and more pink on the belly. The lower mandible of *T. subulatus* lacks the black tip found in *T. angustirostris*. Vocalizations are the only thoroughly reliable way to distinguish these species in the field, especially in areas of sympatry, although behaviorally *T. angustirostris* is the more active bird (Chap. 6).

Many morphological differences within the family will be considered later as they relate to behavior and evolutionary pathways (Chapter 15). A few important points are mentioned below and summarized in Table 1.2.

Size

The wing of the five species ranges from 42.8 to 50.3 mm; the Cuban and Puerto Rican Todies are the smallest and the Broad–billed is the largest. Specimens in the United States National Museum of *T. subulatus* from Gonave Island (off west coast of Haiti) are slightly smaller than mainland todies, but this may not be a statistically significant difference.

Weight

Limited data indicate *T. mexicanus* weighs about 5.4 gr and *T. todus* 6.4 gr. The remaining species are estimated to range from 5 to 7.5 grams.

Bill Dimensions

The smallest bill is found in the Cuban Tody and the largest in the Broad-billed. The bill widths of the two Hispaniolan species (*subulatus* and *angustirostris*) differ more from each other than from any other combination of the five species, a statistic with important evolutionary significance (see Chap. 15). Similarly, the bill lengths of these two species diverge greatly from those of other species.

Red Gorget

The characteristic scarlet bib of all todies (whitish in *T. subulatus*, where a small mandibular "beard" is present) has been the source of interest and curiosity to many naturalists. Attewell (1907) suggested it had a role in feeding as an insect lure. Before I began field work colleagues at Cornell University helped me to test whether the red gorget reflects ultraviolet light, which might attract insects to it, as in some flowers (Eisner, et al., 1969). The results on museum specimens were negative. Furthermore, todies typically search for stationary insects on leaf undersides and their food includes virtually no nectar-sucking prey of the type that are normally attracted to red flowers (see Chap. 6). Although Attewell's idea sounds reasonable, it is undoubtedly fallacious.

Sexual Dimorphism

Todus is basically a sexually monomorphic genus, but the following observations deserve comment.

Wetmore (1916) suggested that iris color in *T. mexicanus* might be correlated with sex. My observations support this; males almost exclusively possess slate irides while they are whitish in females. However, I once saw a "male" (identified by behavior) with a white iris, and one specimen from the Carnegie Museum is labelled "male, iris white." Field observations of displaying and courting pairs, and data from museum skins, indicate that iris color is not necessarily related to sex in the other four species. In the Cuban Tody there is a strong correlation between eye color and sex (Table 15.1), but the tendency is less pronounced than in *T. mexicanus*. In the two sympatric Hispaniolan species there is no relationship between eye color and sex but the color of each species does differ and seems to serve as a reproductive isolating meachanism. In the Jamaican Tody eye color is unpredictable.

A detailed study of iris color in four species of large, closely related Arctic gulls (*Larus*) by Smith (1967) may be relevant here. It was found that species breeding sympatrically have evolved marked differences in iris color (dark or light), while in allopatry their irides are variable. He concluded that female gulls chose males that look like themselves (because they themselves look like their parents), simply as a result of imprinting. As these gulls are otherwise morphologically similar, they apparently recognize subtle visual signals such as iris and eye-ring color, thus preventing hybridiza-

tion. In allopatry, reproductive isolation is no problem and hence there is little pressure to evolve and maintain these differences.

A similar mechanism may explain the pale irides of *T. angustirostris* and dark ones of *T. subulatus* in Hispaniola. Where only one *Todus* is present on an island, two situations appear to have arisen, viz., either the iris color is random, as in *T. todus* (Jamaica), or it is strongly sexually differentiated, as in *T. mexicanus* (Puerto Rico) and *T. multicolor* (Cuba).

It is also probable that iris color is correlated with age; the eyes of the 60 *T. mexicanus* nestlings and fledglings of both sexes that I studied were slate-colored.

Although not useful as a field mark, males of the Jamaican Tody exhibit a more distinct blue-gray subauricular patch than do females; it appears to be absent in juveniles. Sharpe (1874) suggested that this patch of color may be a breeding season phenomenon. However, examination of 10 skins seems to indicate that once *T. todus* attains adult plumage, the sexes retain this color difference; more data are needed before a positive conclusion can be drawn.

In *T. multicolor* and *T. mexicanus*, principally, the blue feathering of the wrists appears to be more colorful in males than females (Table 15.1). On an arbitrary scale of 0 to 3, in order of increasing blue coloration, I found that male *T. mexicanus* specimens averaged 1.9 and females 1.2. Again, this character is not useful in the field.

It may be significant that of 104 specimens of *T. mexicanus* examined the three that possessed a few pink-orange flank feathers were males.

2
DISTRIBUTION

The five species of *Todus* are confined to the Greater Antilles (Map 2.1). A preliminary comparison of their estimated population densities in major habitats is given in Table 2.1.

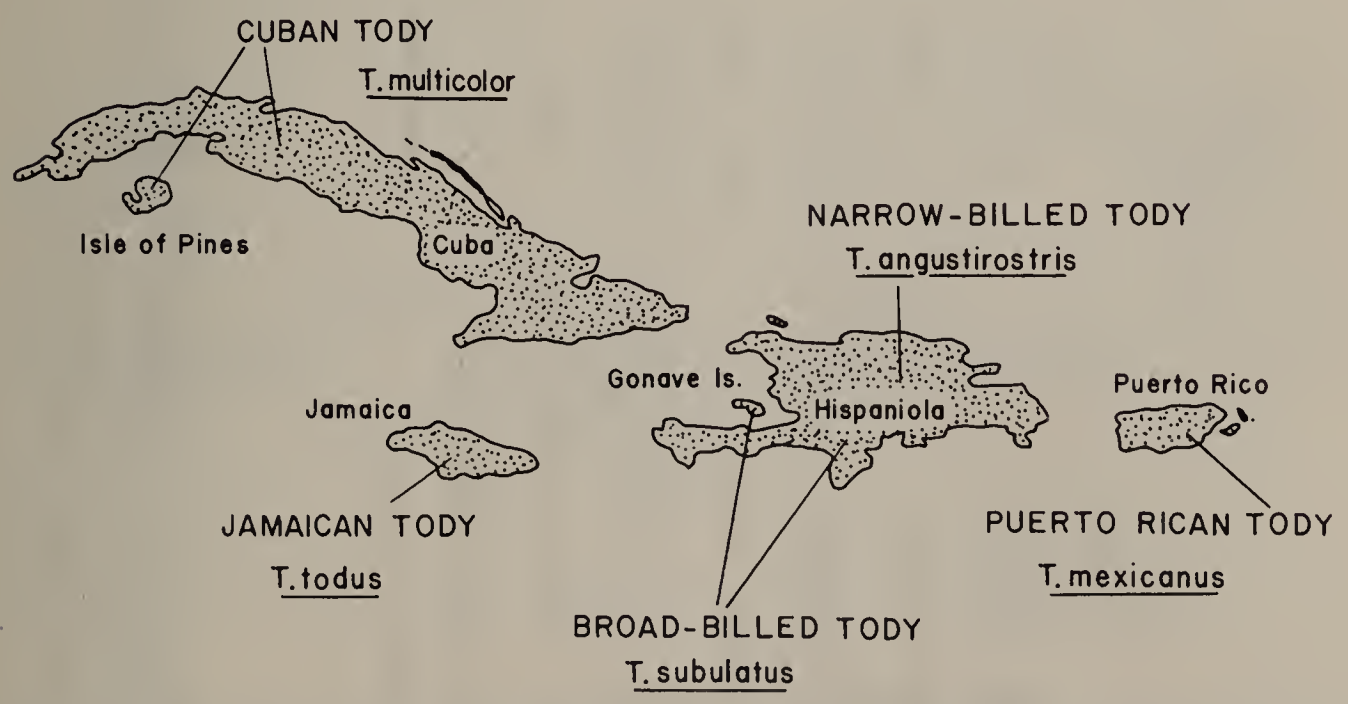
Cuba and Isle of Pines: *T. multicolor*

Although my field experience on Cuba was limited, it appears that this tody is as adaptable ecologically as the other species. From beach thickets of seagrape (*Coccoloba uvifera*, Polygonaceae), it ranges through shrubbery and arid scrub to high montane rainforest (Daniel, 1902; Barbour, 1943; Bond, 1956). It is noteworthy that utilization of the shoreline habitat does not seem to occur on other islands.

The 84 museum specimens studied were collected from widespread localities and habitats up to 2480 m in the Sierra Maestra, the highest mountain range.

Jamaica: *T. todus*

Todies commonly inhabit scrub and forested areas throughout Jamaica, occurring in second-growth, virgin vegetation, or even in much-disturbed habitat (Gosse, 1847; Attewell, 1907; Lack, pers. comm.; this study). The primary habitats, in approximate order of decreasing utilization, are: mesic limestone forest; dry limestone forest (karst, "cockpit country," or "haystack hills"); montane forest; shaded coffee plantations (these now have been mostly replaced by unshaded ones, unsuitable for todies); and mangroves



Map 2.1 Present distribution of the Todidae.

TABLE 2.1

ESTIMATED DENSITIES IN MAJOR HABITATS, AS DETERMINED BY ONE-KILOMETER STRIP CENSUSES [1]

HABITAT	CUBA [2]	JAMAICA [2]	HAITI [2]	DOMINICAN REPUBLIC [2]	PUERTO RICO [2]
MONTANE RAINFOREST	not studied	0 - 6	not studied	6 - 16	0 - 28
MONTANE PINE FOREST	not studied	habitat absent	none	8 - 18	habitat absent
COFFEE PLANTATIONS (*cafetales*)	not studied	sparse	not studied	6 - 10	13 - 31
DRY LIMESTONE FOREST	locally common	4 - 14	rare	0 - 30	3 - 36
WET AND MESIC LIMESTONE FORESTS	not studied	up to 16	habitat absent	habitat absent	10 - 20
BEACHES, BORDERED BY SEA - GRAPE	present	none	none	none	none
SECOND - GROWTH PASTURES AND RIPARIAN WOODLAND	locally common	uncommon	rare	common	common (up to 30)

1) Except for Puerto Rico, where intensive studies were made (244 censuses on 39 trails, every month of the year), table is based on one or two early morning censuses, plus incidental observations at other times, in each habitat on each island, for a total of 27 censuses during January - May, and August.

2) For study sites, see Appendix I and Maps

(only known area is at Point Morant in the southeast in Black Mangrove, *Avicennia nitida*).

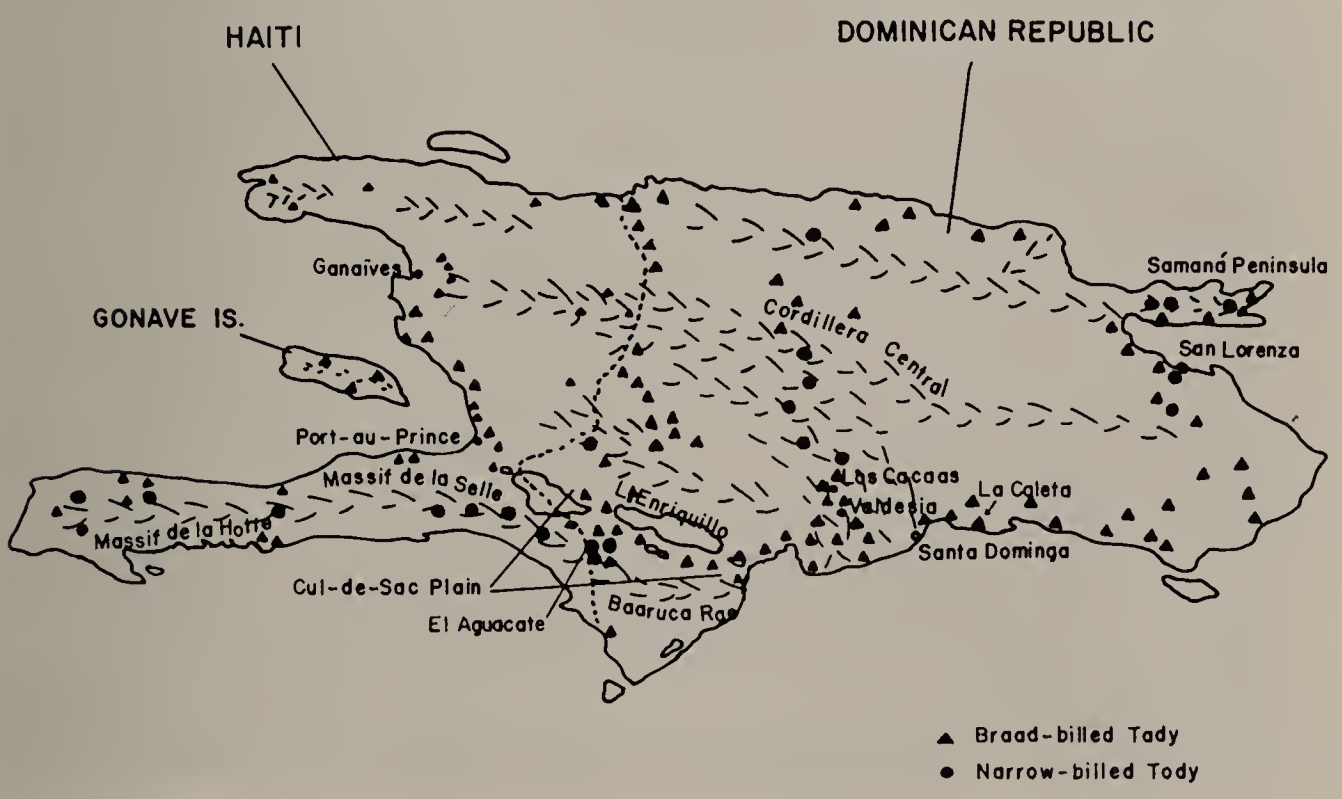
On the whole todies are less abundant in Jamaica than in similar habitats in Puerto Rico and the Dominican Republic (Table 2.1). Possibly this is because of the island-wide limestone formation which is characterized by large rocky outcrops, impenetrable soil, and banks with little or no soil covering, thus affording todies few areas suitable for nesting.

Lack (pers. comm.) and islanders told me that todies are most conspicuous during spring and summer; in other months they are generally silent and their true numbers cannot be appreciated. As I was in Jamaica during the period of territorial delineation and courtship, and as the weather was favorable on each census, my figures doubtless represent maximum population densities.

Hispaniola: *T. subulatus* and *T. angustirostris*

The presence of two species of tody on Hispaniola can best be explained geologically. Until as late as the Pleistocene a great ocean-covered trough separated the mountainous southwestern peninsula (Massifs de la Selle and de la Hotte and the Baoruco range) from the main island mass. Today this is the Cul-de-sac Plain, which averages less than 50 m in elevation. It is virtually a desert, containing several sizeable saline lakes, the largest being Lake Enriquillo, which is approximately 40 m below sealevel (Wetmore and Swales, 1931).

The three avian species pairs on Hispaniola (Palm Tanagers, *Phoenicophilus;*



Map 2.2 Known distribution of Broad-billed (*T. subulatus*) and Narrow-billed (*T. angustirostris*) Todies in Hispaniola. Based on this study, Dod (pers. comm.), Wetmore and Swales (1931), Schwartz (1970), and specimens (N = 109).

Ground Warblers, *Microligea;* and *Todus*) suggest that evolution occurred when Hispaniola was separated into two islands. Even today the Gray–crowned Palm Tanager (*P. poliocephalus*) is restricted to the southwestern peninsula, while the black–crowned species (*P. palmarum*) is elsewhere.

Most bird genera seem to have existed since before the Pleistocene (Welty, 1962), and it is conceivable, therefore, that *Todus* reached the two Hispaniolan islands before the Pleistocene, differentiated in isolation, and subsequently intermingled when the islands became united. Today the Hispaniolan todies are separated by habitat and elevation rather than geography. Their known distributions are indicated on Map 2.2.

Sympatry

It has generally been assumed that todies are sympatric only on and near the Samaná Peninsula of the Dominican Republic (Wetmore and Swales, 1931). This eastern arm of Hispaniola has only recently become connected (or is in the process of becoming disconnected—theories differ) to the mainland. The junction is comprised of extensive mangroves which adjoin wet forest and palm swamps. Elsewhere the latter two habitats are typically found only at high elevations (Dod, pers. comm.). The Samaná Peninsula is the sole known location of mangrove-inhabiting todies.

I felt that another possible location for sympatry would be the southwestern slopes of the Dominican Republic leading from the Cul-de-sac Plain up the Baoruco range (Map 2.2), which reaches a height of 2,680 m. This

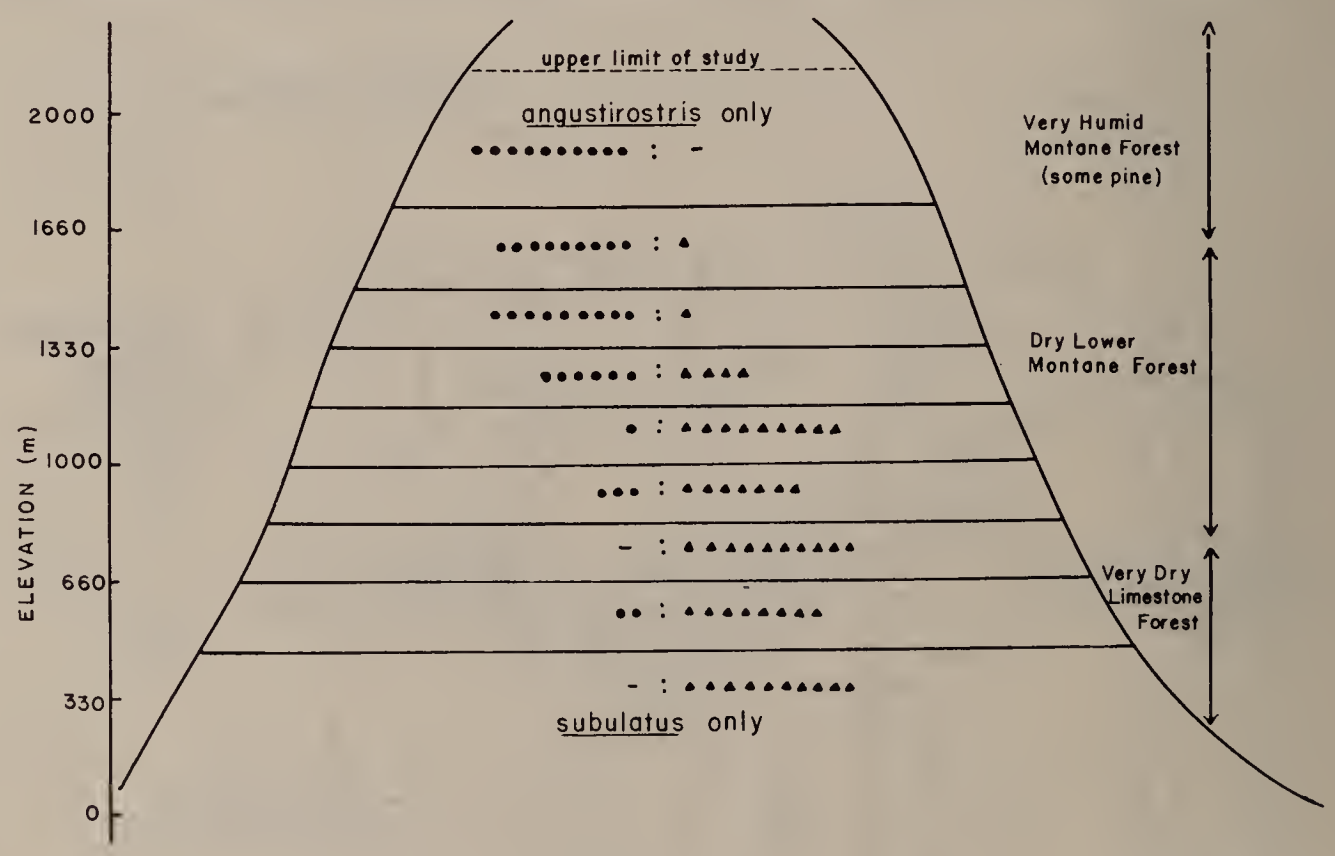


Fig. 2.1 Diagrammatic representation of a portion of the Baoruco Range, Dominican Republic, showing extensive habitat overlap of *T. angustirostris* (dots, N = 130) and *T. subulatus* (triangles, N = 154). Zone of sympatry extends from 465 to 1,730 m.

region is extremely remote, very sparsely populated, and seems not to have been previously studied ornithologically. The vegetation is relatively undisturbed (although we were at an abandoned logging camp) on the Dominican side. I worked six days here, covering the region by car and foot from the arid shore of Lake Enriquillo up to rainforest at 2,100 m. On the mountain leading up to and beyond El Aguacate both todies are sympatric over an altitude of *at least 1,265 m* (Fig. 2.1). That todies occupy such

FIG. 2.2 Very humid montane forest in the Baoruco Range, Dominican Republic, showing pines, *Pinus occidentalis;* 1,700 m. Primarily the habitat of *T. angustirostris* but also the upper limit of *T. subulatus.*

a broad overlap zone is remarkable, as is the variety of habitats they encompass.

Within an altitudinal span of about 2,000 m, there are three major habitats and sympatry between the two todies occurs in all three zones, which are considered below (terminology from Tasiaco, 1969):

1. Very Humid Montane Forest (Including Stands of Pines, *Pinus occidentalis*)

This impenetrable forest contains an abundance of epiphyte–laden mesophyllous trees and shrubs (canopy 6 to 9 m) profusely carpeted with razor-sharp bamboo grass (*Arthrostylidum* sp.), especially at the sides of trails and roads. Within this zone are some pines; under the pine stands, forming a discontinuous canopy up to 19 m from the ground, is often a 4 to 5 m subcanopy, below which is tangled vegetation (Fig. 2.2).

The Narrow–billed Tody typically inhabits the very humid montane forest, keeping well hidden in the dense tangles. Above 1670 m I saw only the Narrow–billed Tody, but at the lower edge of the zone, from 1670 to 1500 m, a few Broad–bills were seen foraging in sunny, rather exposed clearings. Here there was a ratio of 10 *T. angustirostris* to one *T. subulatus,* but this is definitely marginal habitat for *T. subulatus* (further discussed in Chap. 6).

2. Dry Lower Montane Forest (Humid in Ravines)

This is the chief region of overlap by the two todies. This zone includes transitional forest and dryish scrub (canopy one to 4 m) dominated by the sumac-like *Brunellia comocladifolia* (Brunelliceae), *Trema* spp. (Ulmaceae), large herbs such as *Bocconia frutescens* (Papaveraceae), microphyllous legumes and shrubby saplings, vines, and grasses. In the dry scrub Broad–billed Todies feed relatively high in the canopy, while Narrow–bills skulk in the low scrubby vegetation. In humid ravines, where mosses and epiphytes are more abundant and trees grow to 10 m, *T. angustirostris* feeds alone.

The relative numbers of the two todies varies in this zone according to the exposure of the slopes and presence of ravines, but the Narrow–bill diminishes markedly after leaving the wet pines and the rainforest. From a 6 to 4 ratio at the upper limit of this zone I encountered fewer and fewer Narrow-bills as I moved lower, until at 800 m I found none. However, somewhat farther down the mountain, in the third vegetation zone, I again found *T. angustirostris* occasionally.

3. Very Dry Forest (Verging on Subdesert)

This highly arid scrub (Fig. 2.3), with a canopy 4 to 5 m above the ground, is dominated by leguminous trees (*Mimosa, Cassia, Acacia*) and microphyllous, small-fruited shrubs such as Lignum Vitae (*Guaiacum officinale,* Zygophyllaceae), and Gumbo Limbo (*Bursera simarouba,* Burseraceae). It takes on a desert-like appearance because of numerous towering Century Plants (*Agave,* Agavaceae) and scattered cacti (*Cephalocereus,* Cactaceae). This is typical *T. subulatus* habitat, but it harbors occasional individuals of *T. angustirostris*

FIG. 2.3 Very dry forest, southern Dominican Republic, typical habitat of *T. subulatus,* but also inhabited occasionally by *T. angustirostris* at the lower limit of its range.

as low as 470 m. At 530 m I found a ratio of one *T. angustirostris* to 4 *T. subulatus.*

Sympatry is possibly more common than previously suspected in some regions of the Cordillera where different habitats merge. For example, at the headwaters of the Río Isa in the southern Cordillera, I found the Broad-bills extending up to 1070 m in dryish ravines and pasture borders and the Narrow-bills descending to 1130 m in lush ravines, the two species

separated only by a 100-meter wide grazed slope. Wetmore and Swales (1931) also found the two species sympatric in the eastern swamps and wet forest, but not elsewhere.

Allopatry

T. subulatus is found on Gonave Island as well as on Hispaniola. It is by far the most abundant and adaptable species. I found it from 40 m

Fig. 2.4 Typical *T. angustirostris* habitat at 2,000 m, Baoruco Range, Dominican Republic. Dense vegetation is festooned with epiphytic mosses, leafy liverworts, orchids, and climbing bamboo-grass.

below sealevel up to 1700 m, in virgin and second-growth forests, as well as in scrub. The previously reported highest altitude was also 1700 m (Wetmore and Swales, 1931). This was in the southern Haitian mountains about 50 km west of my Dominican Republic study area. Therefore, 1,700 m is undoubtedly close to the maximum elevation for *T. subulatus.*

The habitats favored by the Broad–billed Tody, in the approximate order of population density are: *dry and very dry limestone forests (lowland and lower montane; Gonave Island); *shaded coffee plantations; *second-growth of any kind, including low bracken (lowland and montane); pine forest; very humid montane forest; wet lowland forest (only in Samaná area of northeast); and mangroves (only near Samaná). All these habitats are also occupied by the Narrow–billed Tody, but those most favored by Broad–billed Todies are marked by an asterisk (*).

The limestone outcrops in southwestern Dominican Republic are composed of easily workable, chalky, rock-like soil similar to that of Guánica, in Puerto Rico. It is ideally suited for excavation by todies, in contrast to the hard, irregular limestone outcrops in Jamaica, and doubtless has much to do with the relative abundance of this species.

T. angustirostris is generally confined to the wet, high elevation rainforests or pine forests of Hispaniola, where dense vegetation is carpeted with epiphytic mosses, leafy liverworts, orchids, Spanish moss, ferns, and climbing bamboo grass (Figs. 2.2 and 2.4). The species drops to sealevel in the northeast (Samaná Swamp forest) and also is lower in the Baoruco range, chiefly in moist gullies, as noted above.

I found it as high as 2100 m, the upper limit of my studies, but Wetmore and Swales (1931) heard it at 3200 m near Los Arroyos in the Cordillera Central, Dominican Republic, the highest elevation recorded for any tody.

Habitats in which the Narrow–billed Tody is found, in approximate order of population density are: *wet rainforest (including pines), both in the mountains and in northeastern lowlands; dry lower montane forest, chiefly in ravines; very dry limestone forest; coffee plantations (rarely; one shot by Danforth (1929)). In these habitats the Broad–billed Tody is also found, but those most typical of *T. angustirostris* are indicated by an asterisk (*).

Puerto Rico: *T. mexicanus*

This species was the most intensively studied. In order to determine its distribution, abundance, and optimum habitats, to evaluate its niches in different forest communities, and to discover possible mechanisms of population regulation, detailed analyses were made of population densities in four major habitat types, viz., Luquillo rainforest, dry limestone forest, lower Cordillera forest, and moist limestone forest (see Map 1.3). I conducted 244 censuses on 39 trail and crosscountry routes that included representative elevations and diversity of habitats, viz., virgin timber, second-growth forest, ridgetops, and extensive "edges" along roads (Table 2.2; see Appendix 2 for details). Most trails were relatively undisturbed; however, my results

TABLE 2.2

DENSITIES IN FOUR MAJOR PUERTO RICAN ECOSYSTEMS

HABITAT	ANNUAL RAINFALL (MM)	NO. OF CENSUSES	NO. OF 1KM TRAILS	AVERAGE DENSITY	RANGE OF DENSITIES
LUQUILLO RAINFOREST					
Tabonuco Zone	750 - 2500	43	8	10.3	0 - 25
Colorado Zone	2500 - 4500	24	3	4.8	0 - 14
Sierra Palm Zone	2250 - 5000	67	3	2.8	0 - 5
Elfin Forest	over 3800	30	3	1.7	0 - 5
Ridgetops	variable	27	3	10.5	3 - 28
TOTAL		181	20	6.1	0 - 28
DRY LIMESTONE FOREST	750	35	7	16.1	0 - 28
LOWER CORDILLERA FOREST					
Susua Forest	2300	10	4	17.9	6 - 36
Riparian valleys		5	2	23.2	13 - 36
Semi-xeric ridges		5	2	12.6	6 - 23
Coffee Plantations	1800	5	1	25.1	13 - 31
MOIST LIMESTONE FOREST	2000	3	3	14.0	10 - 20

are biased toward high densities as tody territories center on suitable nesting banks, often amply supplied by trail and road cuttings.

An additional four, ill-defined, much disturbed habitats received some attention, but were not treated systematically. These were mangroves, moist and dry coastal forests, second-growth along edges of fields, and pastures. And, finally, 24 offshore islands (Caja de Muertos, Cayo Icacos, the Culebra complex, Desecheo, Mona, Monito, and Vieques) were searched intensively for signs of todies, with negative results in every case. All these islands are hot and dry, generally receiving less than 750 mm annual rainfall, that results in a thorny, xeric plant cover similar to dry limestone forest.

Population Density

Luquillo Rainforest

Undoubtedly one of the most picturesque areas in the neotropics, this magnificent national forest encompasses 11,200 ha of virtually uninhabited, heavily forested territory ranging from 130 m to 1165 m in altitude, with the annual rainfall varying from approximately 1750 to more than 5000 mm (av. 3000 mm). The Luquillo Forest may be roughly divided into four altitudinal zones and a ridge association (see Table 2.2).

1. Tabonuco zone (foothills and slopes below 700 m).—This lower montane forest is named after the tall dominant Tabonuco tree, *Dacryodes excelsa* (Burseraceae), which rises majestically to 45 m or more and was abundant in pre-19th century Puerto Rican lowland forests. It is a large, productive

zone covering approximately 70% of the entire national forest and is faunistically and floristically by far the richest region. The high annual rainfall of 750 to 2500 mm and warm temperatures produce a dense, three–layered forest, best developed on the low, protected, well-drained ridges. It is characterized by isolated stately trees or groups (chiefly Tabonuco), which tower above canopy level to 35 or 45 m, and by a continuous canopy at 18 to 23 m composed primarily of large *Guarea trichilioides* (Meliaciae), *Sloanea berteriana* (Elaeocarpaceae), *Microphilis chrysophylloides* and *Manilkara bidentata* (Sapotaceae), and *Inga* spp. (Leguminoseae). Their thin-barked trunks are commonly clear of branches for more than half their height and many possess buttressed roots. In both the canopy and lower layers epiphytes are quite common and varied, and include woody *Marcgravias* (Marcgraviaceae), ferns (Polypodiaceae), and rosetted *Guzmanias* and *Vriesias* (Bromeliaceae). Beneath the canopy are shrubs, palms, small trees, and saplings that mingle with irregular herb and fern layers extending down to the ground. *Cecropia peltata* (Moraceae) and treeferns (*Cyathea arborea*) are present, indicating the disturbed nature of a large portion of this zone.

The leached clayey soils (chiefly Los Guineos and Catalina clays), although moist, are workable, providing suitable nesting banks for todies. This fact, coupled with an abundance of undergrowth and insects, accounts for the Tabonuco zone having the highest tody density in Luquillo Forest, averaging 10.3/km. Fifty-seven per cent of all nest holes begun were found in this zone, and even though many nests were destroyed by mongooses and landslides, the region was responsible for 78% of tody nest successes in the forest.

2. *Colorado zone (valleys and gradual slopes above 700 m).*—The true Colorado zone comprises about 17% of the Luquillo Forest. This broad belt, lying above and merging with the Tabonuco zone, is characterized by the dominance of *Cyrilla racemiflora* (Cyrillaceae), a tree with dark red, spongy bark (thus its Spanish name "Colorado"). These trees rise to about 16 m, and are large and sprawling, with hollow twisted trunks and branches, each a veritable garden of ferns and bromeliads. Other characteristic trees are *Miconia* spp (Melastomaceae), *Clusia krugiana* (Guttiferae), and Sierra Palms, *Prestoea montana* (Palmae).

The Colorado zone is typically made up of spindly, low-crowned microphyllous trees and saplings entangled with epiphytes (chiefly Marcgravia). Abundant grasses, sedges, a climbing bamboo (*Arthrostylidum sarmentosum*), Creeping Treeferns (*Trichipteris borinquensis*), and prostrate mats of Common Spikemosses (*Selaginella krugii*) form continuous cover over the ground. Many fallen Colorado trees add to the disordered scene and their porous, rubbery, semidecomposed wood serve as tody nest sites on rare occasions. As one passes from Tabonuco to Colorado zones not only is the diversity of vegetation markedly reduced (168 versus 53 arborescent plant species), but the general abundance of birds also drops (average of 117 to 61/km) and avian diversity is reduced (21 to 17 species) (Kepler and Kepler, MS).

As soils are poorly drained, massive networks of tree roots cover the

ground with the result that soil banks are scarce and the density of todies (4.8/km) is half that in the Tabonuco forest.

3. Sierra Palm zone (high steep slopes and ravines, descending to 500 m).—The graceful Sierra Palm (*Prestoea montana* = *Euterpe globosa*) forms pure forests on steep slopes and mixes with *Clusia krugiana* (Guttiferae), *Tabebuia rigida* (Bignoniaceae), various *Miconia* spp. (Melastomaceae), and treeferns (*Cyathea*, Cyatheaceae) in transitional forests.

The maximum height of this single-storied vegetation type is about 17 m; the trunks of thin-stemmed palms are laden with bromeliads (*Guzmania, Vriesia*) and ferns (Polypodiaceae, Hymenophllaceae). It is not a seral stage but a mature forest; its appearance apparently is related more to the rate of erosion than to other factors. The unstable, shallow, well-watered (2250 to 5000 mm rain annually) soils are exceptionally rocky, supporting a sparse but continuous undergrowth of ferns, ground orchids, small shrubs, and herbs.

Todies prefer brushy areas, generally away from rocky streams, where there is an abundance of branches, twigs and leaves. The relatively open palm stands, which also have a very low insect density (Kepler and Kepler, MS) do not afford the preferred habitat. In addition, the banks are composed primarily of hard, rock-like soil which, even when wet, is almost impossible for todies to excavate. In this zone only one fresh and two old completed burrows were found, although many attempted excavations were noted. Consequently, in the Sierra Palm zone the population of todies is very sparse, averaging only 2.8/km. As in all zones above the Tabonuco zone, other avian species are similarly poorly represented (Kepler and Kepler, MS).

4. Elfin forest (isolated peaks and high ridges above 900 m).—Dense vegetation of low stature typifies this zone; a multitude of factors shape the growth habits, tolerance, and degree of entanglement of the relatively few plant species. Reduction of light by almost persistent enveloping clouds, differential exposure to high velocity winds (frequently up to 90 km/hr), reduced temperature, high humidity (av 98.5%), and saturation and leaching of the soils are a few of the most important factors (Howard, 1968).

Stunted trees and treeferns (up to 6 m high) and a high percentage of endemism characterize this almost impenetrable habitat (Fig. 2.5). Botanical species composition is poor, with only two dominant trees (*Tabebuia rigida*, Bignoniaceae and *Ocotea spathulata*, Lauraceae) comprising 70% of the exposed crowns. All vegetation is profusely draped and interwoven with epiphytic mosses, leafy liverworts, ferns, bromeliads, and lianas.

Rainfall is high (over 3800 mm annually), growth rate is slow, insect abundance is the lowest of all tested stations in the forest, and birds are poorly represented both in numbers and species diversity (Kepler and Kepler, MS). Here todies reach their lowest densities, averaging 1.7/km. I found only one completed burrow; the scarcity of burrows is probably due to the waterlogged, sticky, clayey soil subject to frequent slippages, to the occurrence of temporary waterfalls preventing regular visits to the burrow, and to plentiful vegetative growth on all banks. Clouds and rain suppress

FIG. 2.5 Elfin Forest, Luquillo Forest, Puerto Rico. Note the profusion of epiphytic leafy liverworts and mosses, and the indicator treefern (*Alsophila bryophyla*). The forest is enshrouded by clouds for almost 100% of the night and 60% of the day (Howard, 1968).

tody activity and vocalizations (Fig. 2.10).

5. *Ridgetops (Fig. 2.6).*—These variable swaths separating valleys and peaks, range from luxuriant mixed forest to rather stunted elfin forest, depending on their location and exposure. Three ridges at different elevations were studied to cover this habitat diversity. Tody densities averaged 10.5/km, but this figure is not representative of all ridges, as 70% of my censuses

FIG. 2.6 Lush transitional ridgetop vegetation at 800 m, Luquillo Forest, Puerto Rico at La Mina Field Station. Typical trees are the large-leaved trumpet tree (*Cecropia peltata*) and Sierra Palms (*Prestoea montana*).

were conducted on one particularly well-vegetated trail with good soils and abundant trailside nesting banks. Most ridges are impenetrable, steep and rocky. Information on territory size in an area including ridgetops is presented in Chapter 5.

Dry Limestone Forest (sealevel to 230 m)

Guánica Forest Reserve, a 2,800 ha xeric scrubland, lies in the southwest portion of the island (see Map 1.3) in the rainshadow of the Cordillera Central. Canopy height seldom exceeds 7 m and the semideciduous low trees and shrubs are small-leaved and often thorny (Fig. 2.7). Cacti (*Opuntia, Cephalocereus*) are abundant, sometimes forming impenetrable stands, and plant species diversity is the greatest on the island (Woodbury, pers. comm.). Dominant trees include *Pisonia albida* (Nyctaginaceae), Mahogany *Swietenia mahogoni* (Meliaceae), and *Acacia farnesiana* (Leguminoseae).

There is no marked vertical stratification in contrast to the other forests, and lianas and epiphytes are poorly developed except for the "bird's nest" bromeliad, *Tillandsia recurvata.* Despite the absence of fresh water and an average annual rainfall of only 750 m, todies are in great abundance. Quickly and easily they excavate the porous limestone soils of natural banks and along roads and trails.

I spent over 50 days (covering 10 months) working in areas extending from sealevel, where cacti predominate, to the driest ridges, including

FIG. 2.7 Dry season in the Guánica forest, Puerto Rico, along East Road, a census route.

marginal disturbed land. Tody densities averaged 16.1/km, almost three times the average density in Luquillo Forest. Comparing the two forests, we have shown (Kepler and Kepler, 1970) that, for all avian species, Guánica supports over three times the number of birds and over twice the species diversity as does Luquillo. Correlating with this, average insect density is about twice as great in Guánica (Kepler and Kepler, MS).

FIG. 2.8 Ridgetop trail, Susua Forest. Note *Agaves* and typical microphyllous trees (canopy about 6 m).

Lower Cordillera Forest

Two quite different areas were studied in this zone, both offering excellent conditions for todies, in terms of workable soils and abundant epiphytic and understory vegetation, resulting in the highest densities for the whole island. These are the Susua Forest (Fig. 2.8) and coffee plantations.

1. Susua Forest (100 to 450 m).—This 1,320 ha reserve of secondary mesic forest supports a high density of 23.2 todies per kilometer in the cool, lush riparian valleys (canopy 12 to 13 m), decreasing to 12.6/km on the more arid higher ridges (canopy 4 to 7 m). The average for the entire forest is about 17.9/km.

2. Coffee plantations (650 m).—The second area studied in the lower cordillera forest zone was that of coffee plantations (*cafetales*) near Aibonito, central Puerto Rico, during February, July, October, and November. Although cultivated, these plantations resemble second-growth forest in their abundance of understory shrubs, vines, and epiphytes growing beneath shade trees, such as Oranges (*Citrus paradisi*, Rubiaceae), *Inga* spp, and Immortelles (*Erythrina peoppigiana*, Leguminoseae).

Todies averaged 25.1 birds per kilometer, typical of observations in other *cafetales*, and verifying observations by Wetmore (1916) that todies reach optimum density levels in coffee plantations.

Moist Limestone Forest (150 to 400 m)

This karst ("haystack country"), consists of small, rounded, cave-studded limestone hills supporting a luxuriant evergreen forest, and a fairly rich understory of shrubs and epiphytes. It receives about 2,000 mm of rain annually. Dominant trees include mahogany and cedar (Meliaceae), Magas (*Montezuma speciossima,* Malvaceae) and large, leathery-leaved Autograph Trees (*Clusia rosea*, Guttiferae). The basin-like sinks have steep irregular limestone cliffs and slopes, which drop to muggy, circular valleys, supporting tall, broadleaved hygrophytes, evergreen epiphytes, mosses, and fungi. Vegetation on the ridgetops and areas between the sinks is lower, resembling arid parts of the Susua Forest. I studied briefly two karst reserves, Río Abajo and Guajataca (Map 1.3), in which both averaged 14 todies per kilometer, corresponding roughly to one pair in each small valley and two to three pairs in larger ones.

Miscellaneous Study Areas

1. Mangroves.—I checked seven mangrove areas in Puerto Rico: Boquillo Creek, Ensenada Comezon, Espíritu Santo river and outlet, Paraguera including marine "hammocks," Phosphorescent Bay, Piñones Lagoon, and Roosevelt Roads Naval Base (Map 1.3). These locations included freshwater, brackish, and marine mangroves which border on pastures, sugarcane fields, sparsely vegetated dry hillsides, coconut plantations, and beaches. Of the seven areas only two sites near Phosphorescent Bay and one at Parguera held small numbers of todies. At Phosphorescent Bay they were feeding

among Black Mangrove adjacent to Frangipani (*Plumeria alba*), cacti, (*Opuntia*), aromatic *Lantana* (spp.), and other scrubby xerophytes just inland of the swamp. No todies were found in Red Mangrove (*Rhizophora mangle*), whose well-developed prop roots grow in deeper water and which normally do not intermingle with terrestrial plants.

On many occasions I and other observers found todies at Parguera, adjacent to dry unproductive pasture, so I am fairly certain they were not abnormal visitors, although the habitat is marginal.

2. *Moist coastal forest.*—The original double-storied lowland forest (canopy 40 m) has disappeared, the whole area having been cleared during the 19th century and subsequently used for agriculture and housing. Some hillsides, however, have regrown into broad-leaved, second-growth forest, especially in western Puerto Rico. On several occasions I heard todies near rural residential areas, but they are definitely not common garden birds.

3. *Dry coastal forest.*—This *Acacia*-dominated forest is a low, xeric, discontinuous second-growth (up to 10 m high) bordering pastures and fields and covering hilltops and slopes. In any stand of a hectare or more todies are normally heard in varying numbers, depending on the size of the patch, but do not occur in open, sparsely vegetated fields. They also are not found in the northeast corner of Puerto Rico, where the flora and insect diversity and density would seem to provide habitat for them. This may be due to the former widespread destruction of the land for agriculture.

4. *Second-growth, along fields, pastures, and riparian woodlands.*—Entire mountains and valleys are now rapidly developing continuous plant cover, providing new habitat for todies. Wherever small patches of bushes grow and extend outwards, todies take up residence. Riparian woodlands are

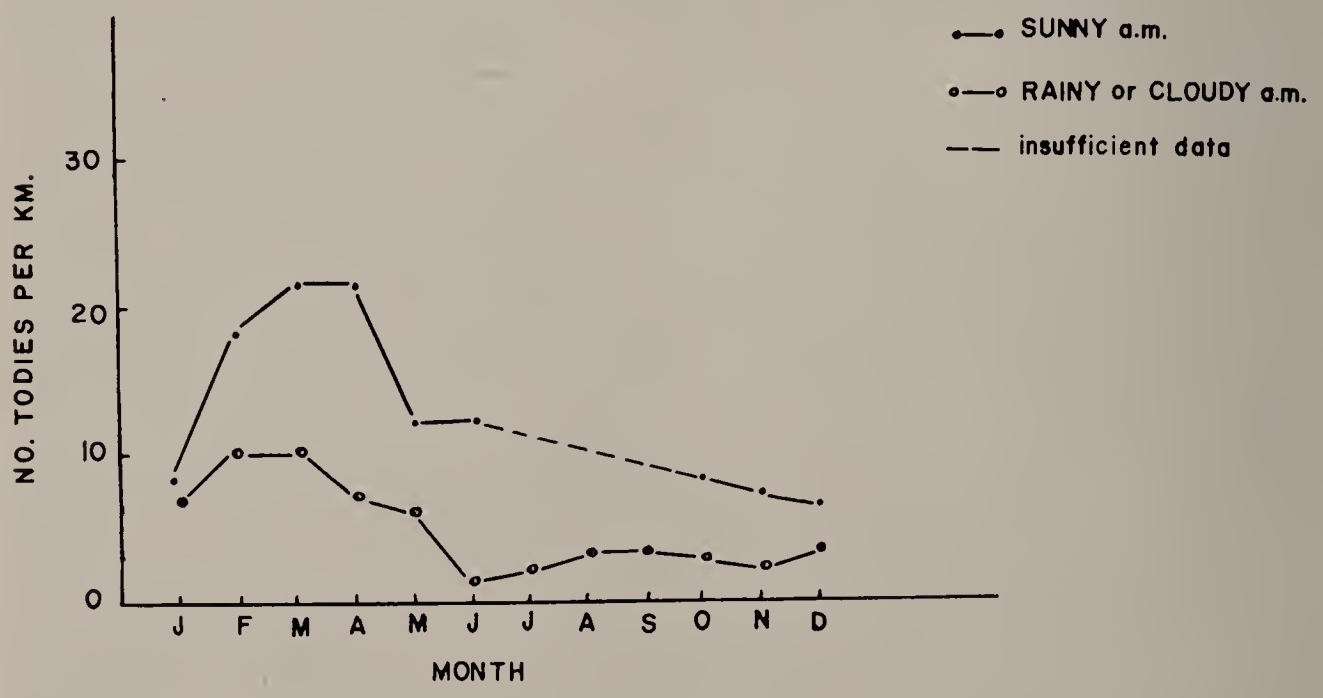


FIG. 2.9 Influence of local weather on tody activity and census results. These data were obtained on El Toro Ridge Trail from 42 censuses during early morning hours (06:30 to 09:00). Each point represents an average of two to four observations. The maximum tody density (linear) was 28/km.

especially rich in plants and their attendant avifuana. Three censuses in riverbottoms and miscellaneous agricultural tracts revealed tody densities of up to 30/km.

Discussion

General Distribution

T. mexicanus exists in most forested habitats, concentrating in Commonwealth and Federal Forests, and generally is absent from coastal areas and offshore islands. It is euryecious, extending from lowland xeric scrub and

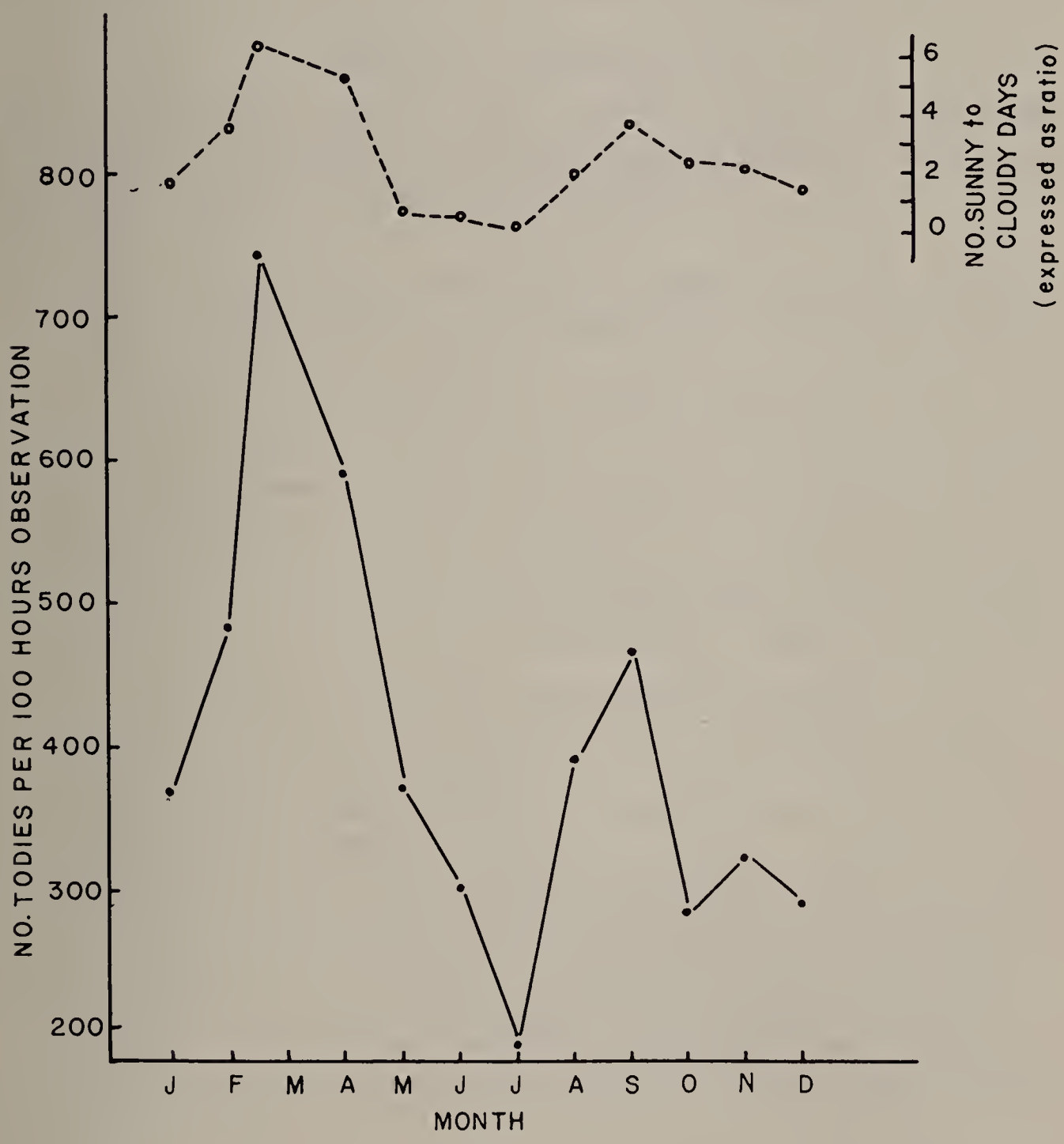


Fig. 2.10 Activity in relation to seasonal weather. Data were obtained from over 1,000 hrs of observation in Luquillo Forest, Puerto Rico, from September 1968 to September 1970. Each point represents the actual number of todies seen or heard per 100 hours of field work.

mangroves to the highest peaks, abounding in lower cordillera forests and *cafetales*. Within the rainforest a striking relationship exists between tody density and increasing altitude; as elevation increases, with its associated vegetational changes, todies decrease in abundance (Fig. 2.9). Overall, the highest densities occur in tall forest at low elevations (Table 2.2), where there are up to 36 birds per linear kilometer.

Todies adapt well to second-growth; in fact, they prefer tangly growth to pure, open stands of forest. Because of this, *T. mexicanus* still thrives in Puerto Rico, despite a human population approaching 2,000/sq/km. The future is also promising for this species, as it is estimated (Woodbury, pers. comm.) that 80% of mountainous cleared land is growing back to forest, as island industry and city life are emphasized.

Effects of Season and Weather

Because the results of censuses are greatly influenced by weather (Fig. 2.9) and the season of the year (Fig. 2.10), samples over a minimum of two years are necessary to determine the densities of populations in most habitats. It will be noted in Figures 2.9 and 2.10 that activity is greatest during the two "dry" seasons (the February-to-April spell coincides with courting, nest-building, and delineation of breeding territories).

3
VOCALIZATIONS AND WING-RATTLING

Adult Volcalization in *T. mexicanus*

I identified six distinct sounds made by the Puerto Rican Tody. The calls, even though unmusical, and the peculiar bobs that accompany them, constitute some of the most characteristic qualities of todies.

The birds are most vocal from February to May, when their full repetoire may be heard. Cloudy and rainy days suppress their activities as well as the vocalizations, making them much less conspicuous (Fig. 2.10).

Each sound is discussed below, and an attempt is made to symbolize it in musical notation. The Beep and Loud Beep are year-round vocalizations; Bee-beep, Beep-trill, Muttering, and Gutteral Feeding Call are almost confined to the breeding season. Visual displays accompanying these sounds are only mentioned, as they are discussed in Chapter 5.

Beep

The Beep (♪) (Fig. 3.1a), a contact call produced all year by both sexes, is the most commonly heard sound and is uttered at a rate of about one/sec. It is a single short note, somewhat resembling warbler call notes, which is audible at a distance of about 50 m. It is heard under the following circumstances, each determining the call's sharpness, intensity, and frequency: foraging, chasing, entering a burrow, contacting an incubating partner in readiness for change-over, and responding to a disturbance. Sometimes members of a pair have tonal variations (slightly higher and lower pitches).

This is the only sound that can be subdivided into recognizable subgroups:

1. The "*regular*" *Beep* is given during foraging (regardless of the distance between members of a pair), during low intensity intra- or interspecific encounters, just before takeoff, and after landing.
2. Very low-pitched, muffled *low Beeps* may be heard as todies approach their burrows (empty or with eggs or young).
3. *Sharp Beeps* are loud, staccato, and have an "urgent" quality. These are rendered as signals for danger, especially when adults with food are searching for fledglings, or as contact calls between partners inside and outside nests.
4. *Accelerated Beeps,* often accompanied by short active flights, Wing-rattles, rapid Bobs, and other fast vocalizations, are uttered during periods of excitement (aggression, protection of young from potential predators, fledging of nestlings).

Loud Beep

This sound (Fig. 3.1b) is of greater intensity, more nasal, more emphatic and harsh, and about three times longer (♩.) than the Beep. It is a component

VOCALIZATIONS AND WING-RATTLING

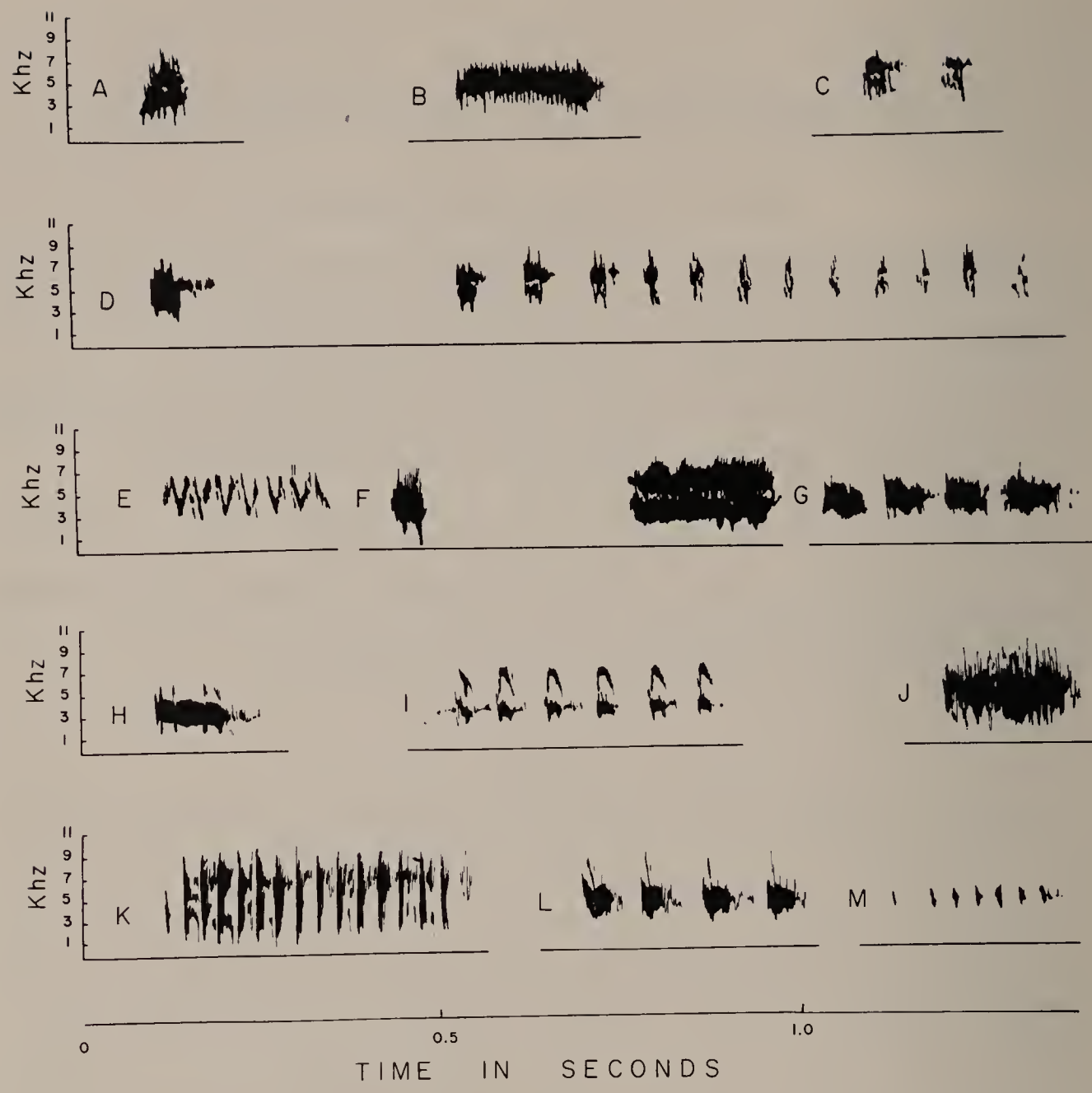


FIG. 3.1 Sonagrams of vocalizations and Wing-rattling of adults and juveniles.

a) Beep of *T. mexicanus;* typical contact call.
b) Loud Beep of *T. mexicanus;* a loud, buzzy, nasal sound given when todies are disturbed.
c) Bee-beep of *T. mexicanus;* a fast double call given when todies are agitated, especially during breeding months.
d) Beep-trill in *T. mexicanus;* a short Beep followed by a downward trill, given primarily when caring for fledglings.
e) Purring trills of 11- and 12-day nestlings of *T. mexicanus.*
f) *Chip chee;* typical two-part call of *T. angustirostris.*
g) *Chippy chippy chippy chip* of *T. angustirostris;* a loud, chattering vocalization heard during hostile encounters.
h) *Terp terp terp terp* of *T. subulatus;* a characteristic monotonous, whistled call uttered in a complaining tone and repeated indefinitely.
i) Chattering call of *T. subulatus;* given when agitated.
j) Loud Beep of *T. todus;* a characteristic loud, nasal, buzzy call.
k) Throat-rattle of *T. todus;* a rapid guttural sound similar to Wing-rattling, given during territorial encounters.
l) Four-part whistle of *T. multicolor,* a characteristic note.
m) Wing-rattling; a rapid, whirring sound produced by all species, especially during the breeding season.

of territorial displays and is often associated with Wing-rattling, Bee-beeping, and Bobbing. It is produced almost entirely by slate-irised "males".

Cory (1885) likened a Puerto Rican Tody vocalization (presumably this one) to "the snort of a pig." However, to me it more closely approximates the "peents" of Common Nighthawks (*Chordeiles minor*) or of Woodcocks (*Philohela minor*). It has also been described as "pree" (Wetmore, 1916) and "cherek" (Bond, 1971), but despite the latter's designation, it is a monosyllabic note.

As *T. mexicanus* frequently Loud Beeps after disburbing noises (caused, for example, by people, cars, airplanes, cackling woodpeckers, and squawking parrots), it is the sound one most frequently associates with this species. I often clapped my hands to locate todies; the resulting loud, stressed noise from such a tiny bird often surprised the uninitiated tody-watcher.

The first attempts at this vocalization by juveniles are high-pitched and strained; only after about six months does the call resemble the adult's in pitch.

Bee-Beep

This is a rapid, double Beep (Fig. 3.1c), with a staccato first note followed by a longer accented note (♪♩). When greatly agitated, todies shorten the second note (♪♪♪♪). As in other vocalizations, the bill is opened only slightly while the gorget is puffed out.

This rather sharp sound, audible up to about 150 m, may be given at any time of day, by either sex, and during any weather, but is heard primarily during the breeding season (Fig. 3.2), when it is interspersed between Loud Beeps, Beeps, Beep-trills, and Wing-rattling.

I was able to determine the following underlying functions of Bee-beeps (81% observations, N = 4153):

Communication with Young (N = 2760, 66.6%)

When todies are caring for nestlings or fledglings they Bee-beep excitedly at potential or actual predators (Pearly-eyed Thrashers, *Margarops fuscatus*; Black-whiskered Vireos, *Vireo altiloquus*; mongooses, *Herpestes mungo*), other todies, and nonpredators such as Puertan Rican Emeralds (*Chlorostilbon maugeus*). The call is also employed when coaxing chicks from the nest and when feeding fledglings.

Territorial Defense (N = 478, 11.3%)

Three-quarters of these vocalizations were directed at conspecifics and the balance at disturbances created by humans.

Miscellaneous and Unknown (N = 915, 22.1%)

Todies occasionally Bee-beeped on first arriving near their nest holes, when courting, or while moving as temporary members of feeding flocks.

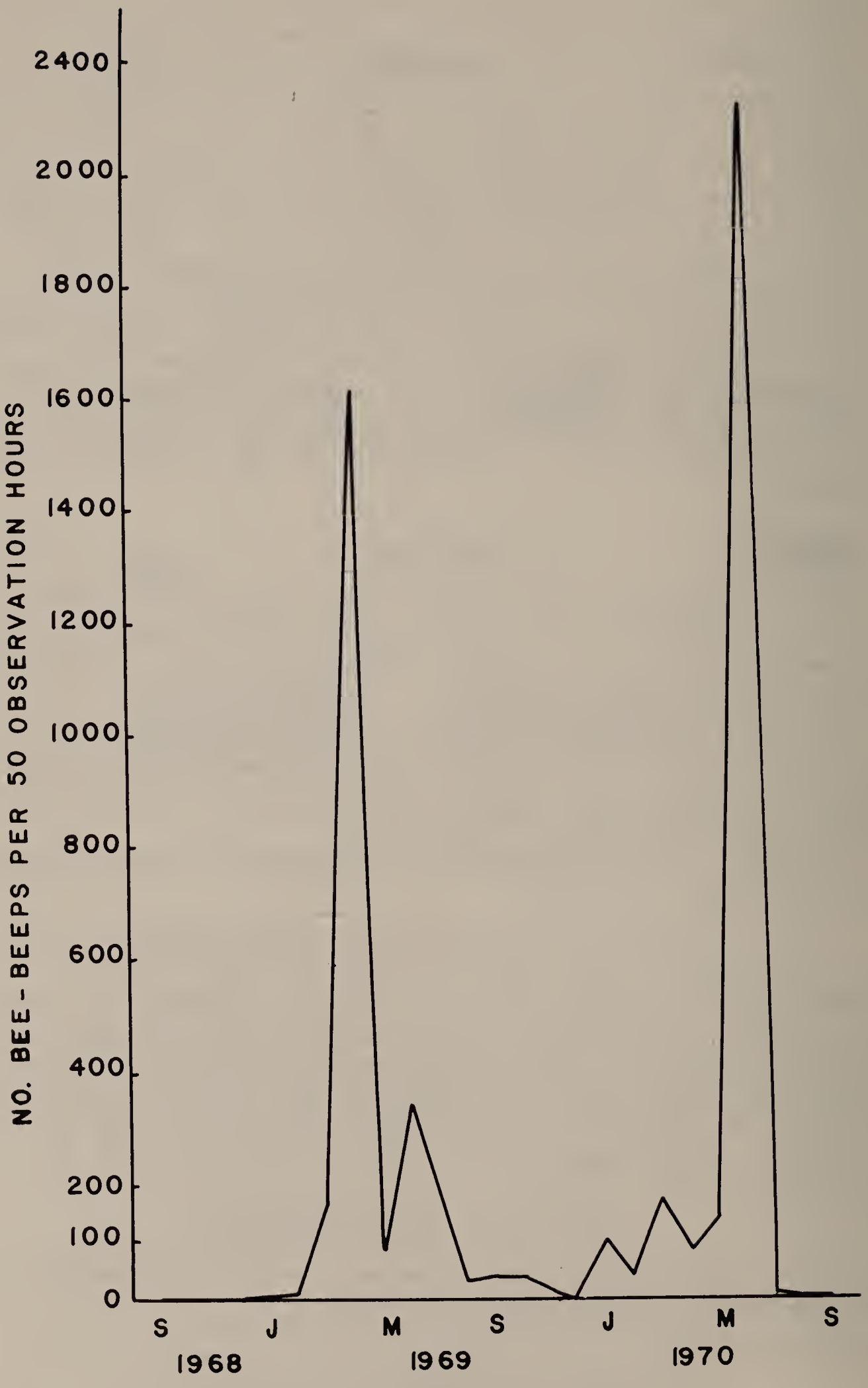


FIG. 3.2 Annual cycle of frequency of Bee-beeping in Luquillo rainforest, 1968–1970; 4153 Bee-beeps were heard during over 1,500 observation hours.

Twice I heard duetting from pairs foraging high in trees; in one instance 17 Bee-beeps and many Beeps were given in perfect unison over a period of three minutes.

Muttering

This very low, muffled, ventriloquistic combination of low intensity Beeps and doubled and quadrupled Bee-beeps, can only be described as a low mutter; individual sounds are virtually indistinguishable. Occasionally one hears rapid, sharp, high squeaks.

While Muttering, the tody does not open its bill, so a slight gular vibration and occasional Wing-flick are the only indications that it is vocalizing. The sound is barely audible and cannot be heard from distances greater than 4–5 m. It is given by both sexes and at any time.

Members of the pair remain close when Muttering. On 35 of 38 occasions (98%) they were excavating nest tunnels. As the major burrowing period is March to May, one would expect to hear Muttering primarily during these months and this is confirmed by the observation that 399 of the 407.7 minutes of Muttering heard during this study were during that period (Fig. 3.3). I found 17 nests near the 22 pairs that I heard Muttering.

Beep-trill

This unmistakable vocalization (Fig. 3.1d) is a short quick Beep immediately followed by a pronounced downward trill ( ). It is almost confined to the breeding season, functions chiefly as an adult-young communication signal, is given by both sexes, and is always accompanied by other vocalizations and by Bobbing.

The functions of the Beep-trills are:

Care of Young (N = 192, 64.1%)

Beep-trills were recorded at nine nests and were given when potential predators were close, when parents were about to feed their young, or when I was banding chicks. The peak of Beep-trilling occurred from April to June, when young were emerging from their burrows.

Intraspecific Interactions (N = 9, 3.1%)

Unknown (N = 98, 32.8%)

Sixty-eight of these calls were given by a single pair with no young. I followed this pair for several weeks, but as I was not near them when they gave the Beep-trill, I could not determine its function.

Guttural Feeding Call

This is an adult version of the squeaks normally given by fledglings. I heard this sound only once. This was when a scrubland juvenile, two

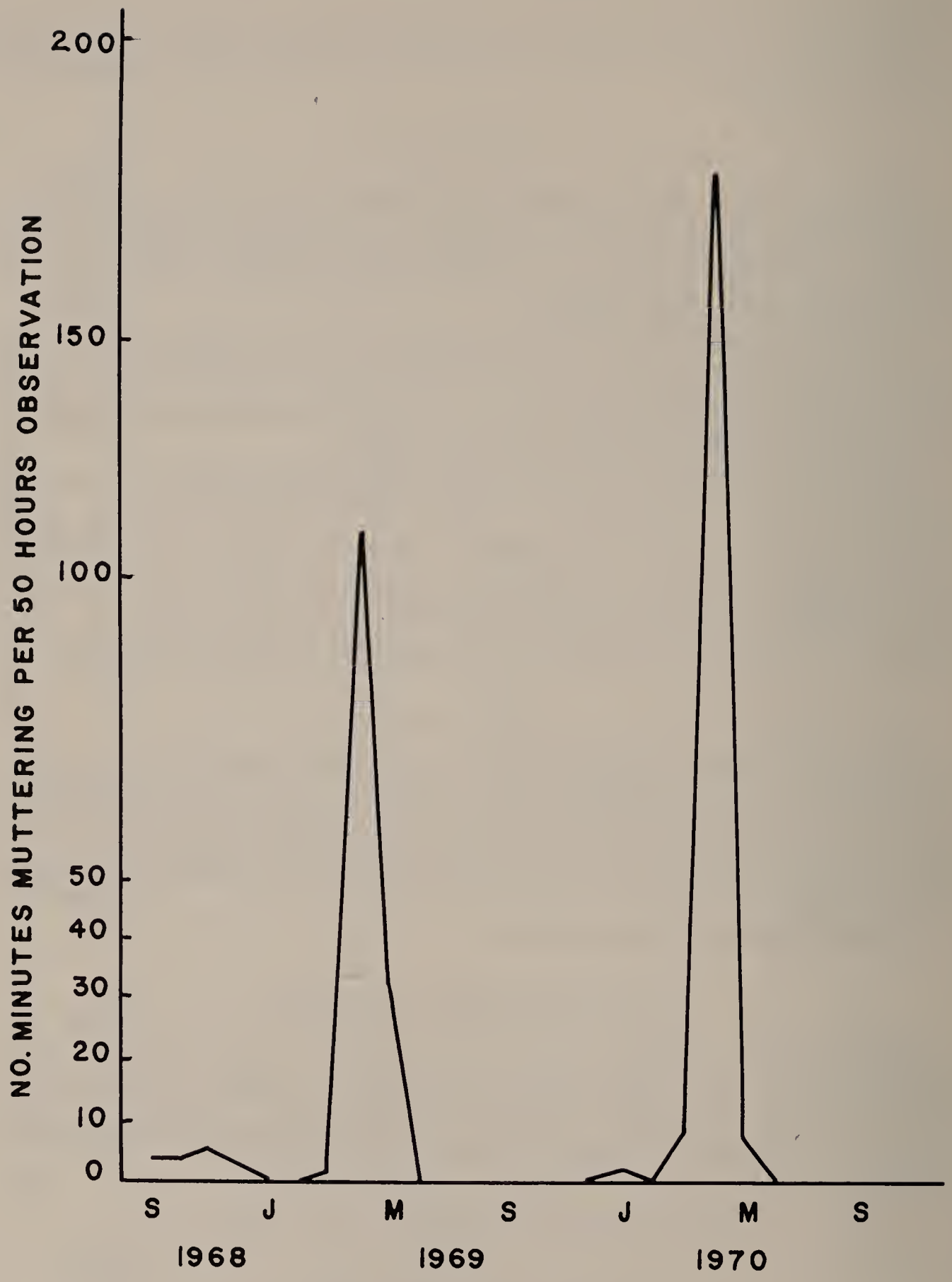


FIG. 3.3 Monthly distribution of Muttering in Luquillo rainforest, 1968–1970. N = 407.7 min of Muttering. Note the association of this sound with months of burrow excavation.

weeks old, had just been fed and was following its parent, which uttered several low guttural calls, eliciting more squeaks from the juvenile.

I occasionally heard guttural sounds from other species of *Todus,* especially *T. todus* (see below).

VOCALIZATIONS AND WING-RATTLING

TABLE 3.1

HOMOLOGOUS VOCALIZATIONS IN THE TODIDAE

VOCALIZATION	*mexicanus*	*todus*	*subulatus*	*angustirostris*	*multicolor*
BUZZY SOUNDS					
Beep	X			X	
Loud Beep	X	X		X	
Guttural Sounds (Beep-trill, Throat-rattle, Guttural feeding call)	X	X	X		
Chattering ("Chippy chippy chippy chip")			X	X	
Chip chee				X	
Bee-beep	X				
CLEAR WHISTLES					
Terp terp terp			X		
Four-part whistle					X
WING-RATTLING	X	X	X	X	X

Juvenile Vocalizations in *T. mexicanus*

At three to four days of age nestlings utter high-pitched squeaks that later develop into loud purring trills, which are especially loud when the birds are hungry (Fig. 3.1e).

When two or three days out of the nest fledglings attempt high–pitched Beeps, which rapidly develop into "regular" Beeps (see also Chap. 11).

Vocalizations in Other Species

For *T. angustirostris, T. subulatus, T. todus,* and *T. multicolor* I present (Table 3.1) only an annotated list of sounds heard, combining the results of this study with those of Wetmore and Swales (1931) and Bond (1971). Comparisons are given where relevant (and note values are based on the standard used for *T. mexicanus*). Table 3.1, although doubtless incomplete, summarizes known homologies; our knowledge of tody evolution would benefit greatly from further comparative studies.

T. angustirostris

I heard four distinct vocalizations from this species in March and April:

1. A frequently repeated, two-part *chip chee* (Fig. 3.1f), accented on the second syllable (♩𝅗𝅥). This characteristic year-round call (Dod, pers. comm.), occasionally varied to *chip chui* or *chic-o-ret,* is the only completely reliable field character distinguishing *T. angustirostris* from *T. subulatus*; the latter's calls are never bisyllabic. It is slower and more deliberate than the *T. mexicanus* Bee-beep.
2. A chattering, trilly *chippy chippy chippy chip* (Fig. 3.1g), dropping in pitch but not in tone (𝅘𝅥𝅯𝅘𝅥𝅯𝅘𝅥𝅯 ♫ ♩). The number of notes varies from three to

nine; most are uttered during Flank Displays, when the accelerated vocalization resembles the *T. mexicanus* Beep-trill.
3. A simple, low, contact *Beep* (♪) somewhat like the *T. mexicanus* Beep. I heard this and the next sound very rarely.
4. A monosyllabic *Beep* (♩.) of the same time, pitch, and duration as the *T. mexicanus* Loud Beep, but less emphatic.

T. subulatus

I heard at least three vocalizations from this species in March and April:

1. A monotonous whistled call, *terp terp terp* (Fig. 3.1h), uttered in a complaining tone (♪♪♪♪), repeated indefinitely. It resembles the Loud Beep of *T. mexicanus* (but less nasal and emphatic) and the four-part whistle of *T. multicolor* (but slower and a little less clear).
2. A trilly, chattering vocalization (Fig. 3.1i), rather like the *chippy chippy chip* of *T. angustirostris*. I heard this only a few times during aggressive encounters.
3. Various guttural sounds, some sounding like the Throat–rattling of *T. todus* and others like the Guttural Feeding Call of *T. mexicanus*; the remainder were single, short and muffled, generally heard during high-intensity displays. These may be confined to the breeding season.

T. todus

Jamaican todies are almost silent during the nonbreeding season; during a week in January and February I heard only two todies vocalize. Rural islanders and Lack told me that they also rarely heard todies except in the spring and summer.

I heard only two sounds from this species during April and May:

1. A *Loud Beep* (♩.), with tones, pitch, and duration similar to the Loud Beep of *T. mexicanus*, but less buzzy (Fig. 3.1j).
2. Throat-rattling (Fig. 3.1k); a rapid guttural sound akin to the Beep-trill of *T. mexicanus* and Wing-rattling. Todies Throat-rattle while perched (as opposed to Wing-rattling), open their bills approximately 3 mm, lean forward, and puff out their gorgets. It is given during territorial displays, accompanying Chasing and Wing-rattling (see Chap. 5).

T. multicolor

The characteristic and only sound I heard from this species was a lively four-part, almost musical, clear whistle (Fig. 3.1l) of similar quality, but faster than the *terp terp terp* of the Broad–billed Tody.

Wing-Rattling

Wing-rattling (Fig. 3.3m) is a whirring sound, similar to the noise heard when pulling one's finger quickly across a comb or to the snapping sound of large flying grasshoppers. It is produced as air passes rapidly through the slightly attenuated outer wing primaries (Wetmore, 1916) and, though

not syringeal, can easily be mistaken for Throat-rattling in *T. todus* (compare Fig. 3.1l and 3.1m). It is a most important element of the tody's repertoire, produced by both sexes, and is normally accompanied by vocalization.

As the vocal repertoire of todies is rather poor, it is possible that Wing-rattling is a partial compensation for lack of syringeal sounds. It assumes great importance during territorial and reproductive displays, as in manakins (Pipridae). Originally described for *T. mexicanus* (Wetmore, 1916), Wing-rattling has since been heard in the whole family (Barbour, 1945; Wetmore and Swales, 1931; this study).

Of 2,027 Wing-rattles noted by me, only 10 were given by perched todies; the remainder were made by flying birds. The sound is controllable, as todies can fly quite silently, in contrast to birds such as the Bananaquit (*Coereba flaveola*) and Hawaiian Apapane (*Himatione sanguinea*) that habitually produce slight wing-whirrs.

The intensity of Wing-rattling varies from a slight whirr to a whip crack almost as intense as in manakins (pers. obser.). Despite its loudness, however, the sound does not carry well and is difficult to record.

Weather appears to have a marked effect on the incidence of Wing-rattling. Throughout the year peaks of Wing-rattling follow peaks of sunny weather and on any given day Wing-rattling is more likely to be heard during clear spells than during clouds or rain.

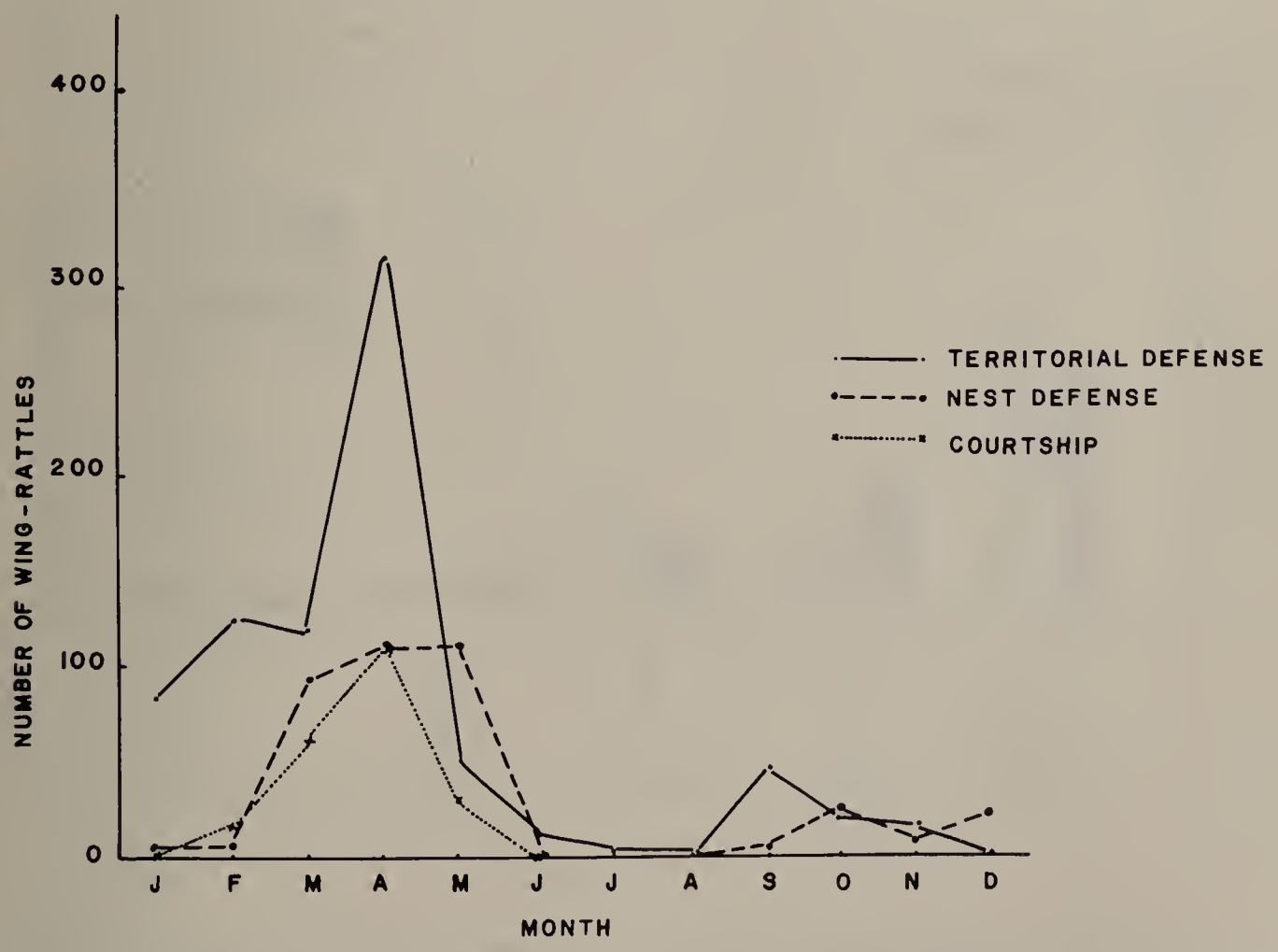


FIG. 3.4 Situations involving Wing-rattling in *T. mexicanus*.

VOCALIZATIONS AND WING-RATTLING

Functions

In the Puerto Rican Tody Wing-rattling occurs in four different situations concerned with territorial or breeding behavior. I could not categorize 5% of the total Wing-rattles recorded in both rainforest and scrub (N = 2027). The relative importance of each group is seen in Figure 3.4, and a breakdown of 1,434 wing rattles into functional categories by month, is presented in Figure 3.5.

The circumstances under which I heard Wing-rattling in the other species of todies seemed similar to those in *T. mexicanus.*

Territorial Defense (N = 1051, 51.6%)

This is by far the most important behavior involving Wing–rattling in *T. mexicanus.* Wing-rattling in this context occurs in every month, but has a steep peak from January to May (Fig. 3.5). The frequency of this behavior is understandable in view of the species' year-round territoriality (see, also, Chap. 5).

These bouts of excitement, at times quite frenzied, involve Chases, Wing-rattles, and loud Vocalizations, and are directed at other todies (823, 79.0%), people (203, 18.6%), Black-throated Blue Warblers (*Dendroica caerulescens;* 17, 1.6%), Bananaquits (5, 0.5%) and Redstarts (*Setophaga ruticilla;* 3, 0.3%).

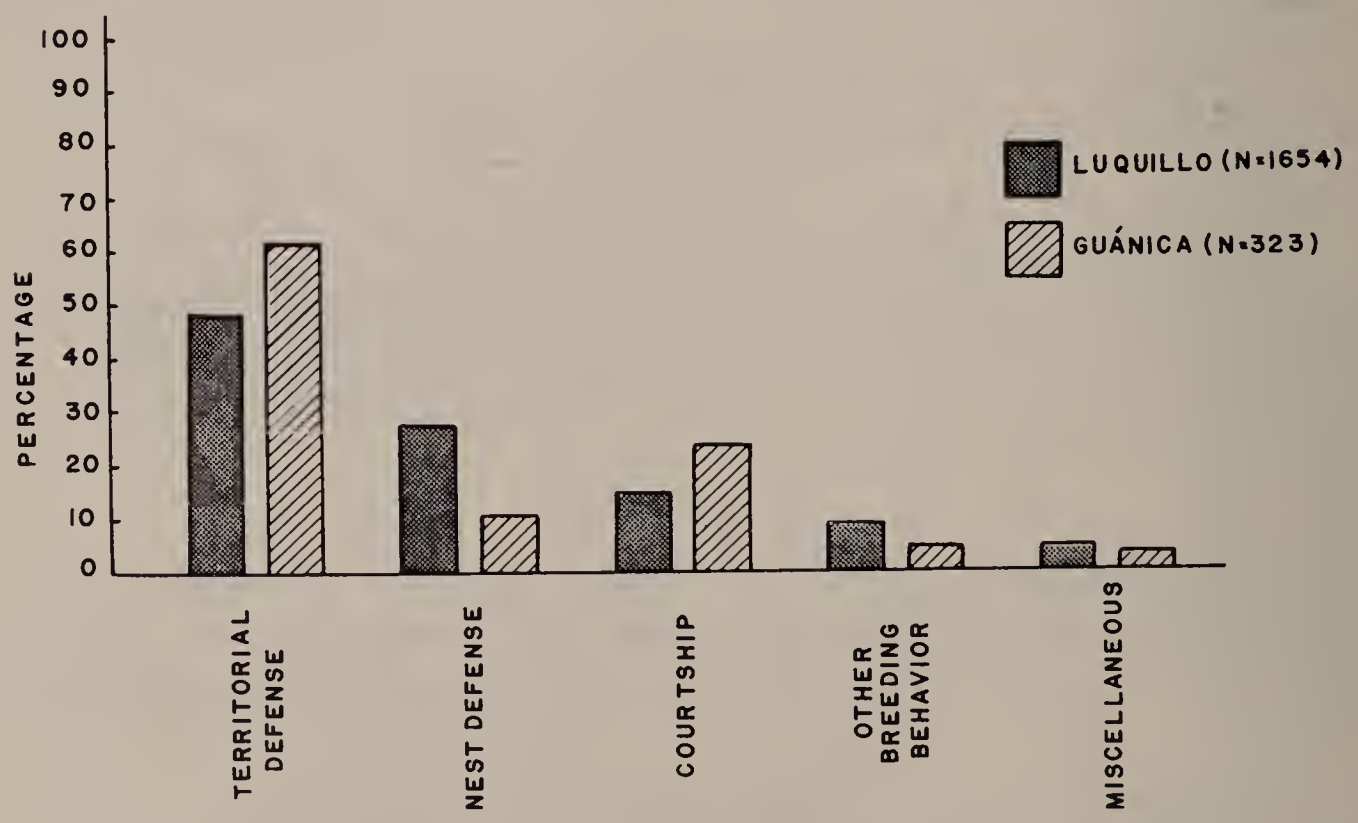


Fig. 3.5 Wing-rattling: annual breakdown of three principal functional categories. Data are from Luquillo Forest, September 1968 to September 1970. N = 1434 Wing-rattles.

Nest Site Defense (N = 451, 22.1%)

At times it was difficult to distinguish nest site defense from territorial defense, thus I included a behavior in this category only if I was aware of nearby nests. Chases were directed at todies (204, 45.0%), people (233, 51.8%), Puerto Rican Emeralds (10, 2.2%), Mongooses (2, 0.5%), and a cow with a calf (2, 0.5%).

Courtship (N = 298, 14.7%)

Wing-rattling is the major element of these displays (see Chap. 8).

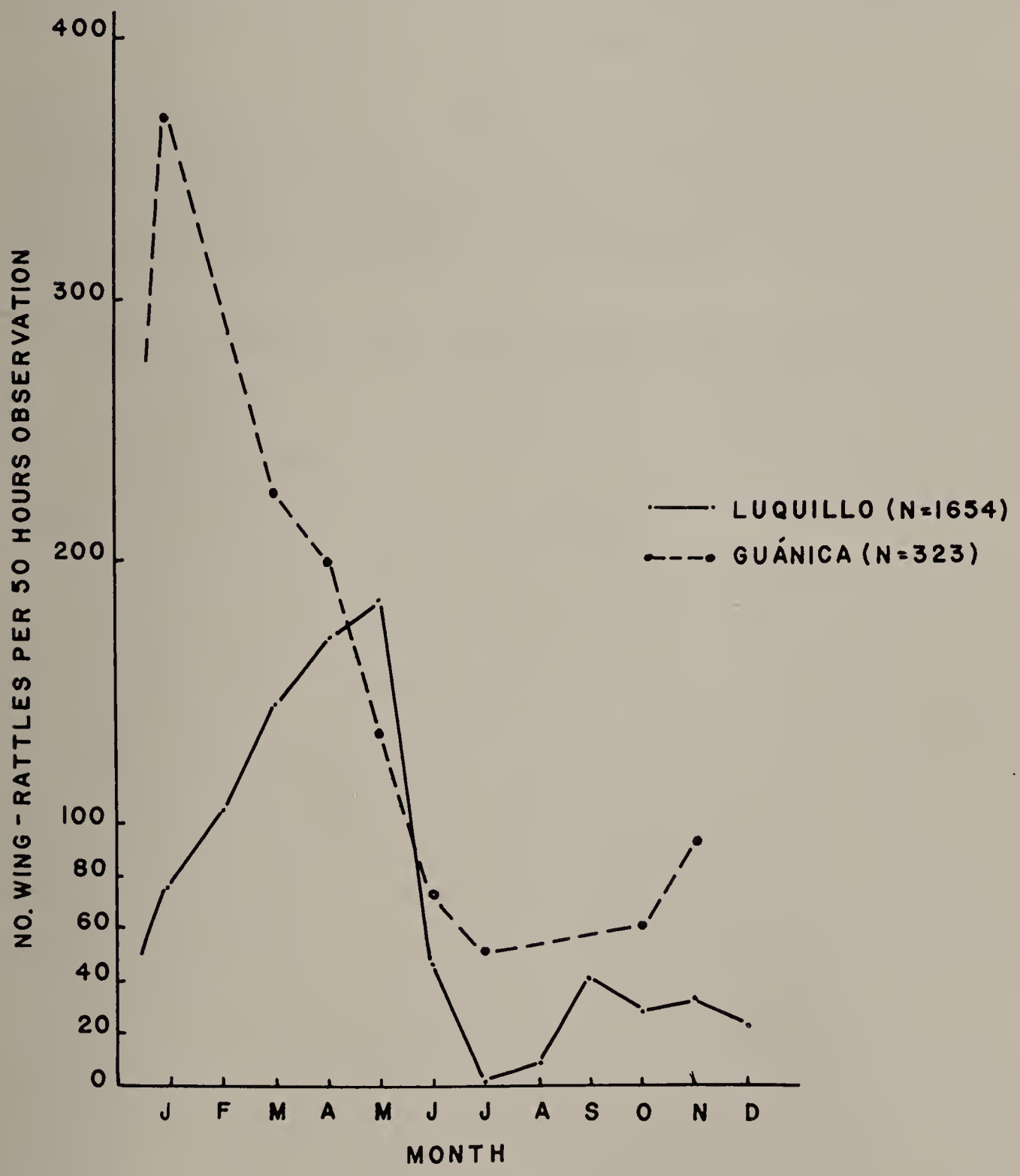


FIG. 3.6 Monthly distribution of Wing-rattling in *T. mexicanus*. Data are from Luquillo Forest (N = 1654) and Guánica scrub (N = 323).

Other Breeding Activities (N = 129, 6.3%)

Todies occasionally Wing–rattle as they fly in and out of their nests, whether they are under construction or are with eggs or young.

When juveniles are first fed by their parents, adults utilize Wing-rattling chases to drive off potential predators and push young off their perches (see Chap. 11).

Miscellaneous (N = 108, 5.3%)

Twice I heard Wing-rattling during Bathing; the remaining times I could not determine the function.

Differences Between Populations

Scrubland todies defend smaller territories and occur in greater densities than do those of the rainforest (Chaps. 2 and 5). Thus it is not unexpected that observations indicate that Wing–rattling is more frequent in the population inhabiting the scrub at Guánica than in that of the Luquillo rainforest (Fig. 3.6). The role of Wing–rattling in population regulation is considered in Chapter 14.

Wing–rattling in other species appears to be identical in sound and occurrence to that of the Puerto Rican Tody.

4
MAINTENANCE ACTIVITIES

Maintenance activities ". . . are concerned with locomotion and the general health and efficiency of the body, mostly occurring throughout the year" (Marler and Hamilton, 1956). In addition to their primary functions, movements involved in maintenance activities often serve as evolutionary precursors to more complex display patterns. Of the 10 categories of maintenance activities discussed below (chiefly from observations on *T. mexicanus*), at least four have been incorporated into agonistic and reproductive activities, viz., Bill–wiping, Fluffing, Preening, and Wing–flicking.

Bathing

Slessers (1970) distinguished four major bathing methods among land birds: (1) standing in the water while bathing, (2) bathing in flight with a dive, (3) moving about in water, and (4) bathing in drizzling rain, dew, or wet foliage. The Puerto Rican Tody uses methods two and four; its short legs are too weak to support active movement in water.

Todies dive into shallow pools from nearby perches, usually just touching the surface as they extend their wings once and smoothly continue their flight, perching momentarily on the opposite side of the pool before returning to their original perch. Sometimes they splash briefly before flying on. After wetting, todies clean themselves thoroughly by Preening, Bill–wiping, Wing–flicking, Head and Body–shaking, and Fluffing.

I saw bathing flights on two occasions; the bouts lasted 5 and 15 min, respectively. The todies entered the water roughly once every three minutes from perches averaging 1.3 m high and 2 to 4 m from the pools. In all cases the bird's angle of approach was less than 45°. Both ponds were small (2 × 1.2 m and 1.3 × 1.3 m), shallow (0.5 to 2 m deep), calm, surrounded by mosses, rocks, and mud, fed by trickling rivulets, and well-shaded by 18 to 19 m canopies. The todies bathed singly but with others nearby, and occasionally rattled their wings when flying between perches. On some flights they did not bathe but fed on tiny midges swarming over the water.

Bathing in drizzling rain, dew or wet foliage may be the more common method. *T. mexicanus* was seen Preening, Shaking, and Bill–wiping during and immediately following rain on eight occasions. They preened vigorously in bouts lasting as long as 10 minutes.

My husband once saw a tody fly up to touch the undersurface of a large leaf, then rapidly drop to a lower perch, catching the drips on its plumage and then preening. We have seen this behavior in Parula Warblers (*Parula americana*) in Luquillo rainforest, and it has been reported in hornbills, budgerigars (*Melopsittacus undalatus*), and the Wren-tit (*Chamaea fasciata*). This specialized bathing behavior has been noted especially in tropical species that seldom or never bathe in standing water (Thomson, 1964).

MAINTENANCE ACTIVITIES

Rain is plentiful in Luquillo Forest and as todies are uncommon near rocky ravines and rivers, I suspect they typically bathe in rain or wet foliage; these are presumably the only methods in arid scrubby regions lacking standing water.

Bill–wiping

Bill–wiping, which apparently has not been previously reported in the Coraciiformes (Clark, 1970), in todies typically involves rapid base-to-tip bill strokes against a perch. Usually they clean both sides of the bill with one to four strokes per side.

I noticed this behavior in four situations. First, while the birds were foraging. As todies constantly feed, squashing insects in their bills or bashing them on twigs, Bill–wiping can be seen at any time, but particularly after a large lepidopteran or orthopteran has been caught. Second, todies generally Bill–wipe after regurgitating pellets. Third, Bill–wiping occurs after body cleaning. Any bout of Fluffing, Shaking, Preening, stretching, tongue-flicking, or Bathing also includes Bill–wiping. And, fourth, it occurs during nest excavation. The clayey soils of Luquillo Forest are usually moist, tending to adhere to the tody's bill and feet, thus necessitating Bill–wiping.

Defecation, Regurgitation, and Bill–Gaping

Todies always defecate while perched by lifting their bodies slightly upwards, pressing downwards and forcing out a rather dry dropping. The adults do not defecate on their nests, although the nests become fouled by the chick's excreta, which are not enclosed in fecal sacs.

When disgorging a chitinous pellet (1 to 2 mm in diameter), the tody opens its bill in a yawning gape, fluffs briefly, stretches its neck upward and shakes its head. Usually upward throat peristalsis alone is sufficient to expell the pellet, but sometimes the tody gapes several times, forcefully ejecting it.

I observed Bill–gaping 40 times, mostly in association with regurgitation, but also during Bill–wiping after a bout of burrowing, feeding, or Preening. Bill–gaping may also stretch the jaws, as has been suggested for Budgerigars (*Melopsittacus undulatus*) (Brockway, 1964).

Drinking

I never saw todies drinking, but it is probable that they obtain water droplets from leaves and insects during feeding maneuvers, as I observed being done by Bananaquits (*Coereba flaveola*) and Puerto Rican Emeralds (*Chlorostilbon maugeus*). Because the Guánica scrubland has no standing or running water, and receives only 750 mm of rainfall annually, the frequent morning dew is probably the only source of drinking water there.

Fluffing and Shaking

During Body-shakes todies first ruffle their feathers, rapidly "roll" their bodies laterally, then relax, allowing their feathers to settle.

They commonly erect or shake only their head feathers, using a jerky sideways movement as, for example, when immobilizing insects, regurgitating pellets, or preparing to fly.

Fluffing and Shaking invariably accompany other behavior, such as Preening and Bathing. Ruffling of feathers over all parts of the body is essential to Preening, during which the bill is inserted among the feather bases. When Bathing, Shaking serves to rid the feathers of excess water in preparation for Preening.

When killing insects, todies thrash them against a perch or flick them in the air with vigorous lateral Head-shakes. Invariably the head is shaken after particularly juicy food is swallowed, apparently as a means of cleansing the feathers. When nesting the plumage becomes dirty and it is frequently Fluffed, Shaken, and Preened.

When facing opponents (conspecifics or otherwise), todies often Fluff their plumage extensively and stand high on their legs in a threat display. This is particularly pronounced in the non-Puerto Rican species (see Chap. 5). Finally, before leaning over horizontally in a submissive posture, females Wing–flick and Fluff, especially their abdominal feathers (see Chap. 8).

Locomotion

As is typical of birds with short, rounded wings, todies normally fly very short distances. A rough correlation between wing length and flight distance may be seen within the five *Todus* species (Table 4.1). *T. subulatus,* with the longest wings, flies farthest and *T. mexicanus,* with the shortest wings, makes the shortest flights. *T. angustirostris* is an exception; even though its wings are relatively "long," it flies the shortest average distance of all species (see Chap. 15 for the evolutionary implications of this).

Apparently the wings of *Palaeotodus emryi* were better developed than those of modern todies, being relatively longer and with larger tuberosities.

Todies sometimes hover when capturing prey from trailside ferns, the undersurfaces or sides of leaves, or from grasses. Occasionally their rapid wingbeats and upright stance reminded me of hummingbirds.

When covering distances of less than 0.15 m, todies either flit (one or two flaps, barely lifting them from the perch), hop sideways, or sidle like

TABLE 4.1

WING LENGTHS OF THE FIVE TODIES AND THE DISTANCES THEY FLY

	subulatus	*angustirostris*	*todus*	*multicolor*	*mexicanus*
WING CHORD (mm)	50.3	46.0	46.0	43.8	42.8
	(N=76)	(N=18)	(N=26)	(N=63)	(N=61)
AVERAGE FLIGHT DISTANCE (m)	2.2	0.8	1.5	1.4	1.3
	(N=419)	(N=417)	(N=277)	(N=404)	(N=3476)
MAXIMUM FLIGHT DISTANCE (m)	40	7	26	19	16

parrots. Fledglings sidle and hop more than adults, as they are reluctant to leave their perches when initially learning to feed. Todies rarely move on the ground (N = 4); but when they do, they hop rather than walk.

Preening

Todies preen in bouts of a few seconds to 10 min by probing and nibbling around the feather bases, and smooth the remiges by running their closed flat bills along them. They pay most attention to the wings and breast, employing additional digging, stroking, poking, and pulling movements, as well as other maintenance activities such as Shaking, Fluffing, Bill–wiping, Gaping, Regurgitating, and Leg-stretching.

Vertical and lateral tail movements used in preening have been incorporated into flank displays of the non-Puerto Rican species.

The birds are silent when preening and often sit high in trees. They favor no particular hour of day but seem to prefer clear weather. Of 30 observations, 20 (66%) occurred on sunny days. As my field work covered slightly more rainy than sunny days, this probably reflects a preference. However, as mentioned under bathing, todies seem to preen deliberately during rain; I once saw them creating their own "rain" by disturbing a large, wet leaf.

The feathers receive most attention during burrow construction; as the breeding season progresses the plumage becomes increasingly ragged and worn as parental activities take precedence over grooming. However, the annual post-nuptial molt soon renews the plumage.

Although lacking direct observations, I suspect that nestlings Preen, as do nestling Redstarts (Ficken, 1962), because I have seen fledglings Body-shake, tuck their bills into the breast plumage, and Bill–wipe within two hours of leaving their burrows.

Scratching

When a tody scratches it brings one leg forward over its slightly drooped wing ("indirect" scratching), tilts its head toward the rear, closes its eyes, erects its crown feathers slightly, and vibrates its foot around the feather bases in the desired area. During this operation, the whole body shakes rapidly. Scratching is always indirect, even when the behavior first appears in 21- to 22-day-old chicks.

Sleeping and Resting

Though rarely seen sleeping and resting individuals typically have ruffled plumage and clasp and sit close to their perches. Todies are not social in their roosting habits and appear to sleep singly within their territories.

At 05:57 on 29 July 1970 in Guajataca Forest, when the light intensity was still so weak I could barely read, I was lying on a trail, staring at the sky filtering through silhouetted leaves, when one "leaf" awoke. The

canopy was 13 m above the ground. At about 10 m there was a tody, fluffed up, perched on a small horizontal twig at the end of a limb. It lifted its bill from beneath one wing, shook its body twice, preened a little, and sat silently before flying off. It was 8 min before I heard todies feeding in the lower brush.

In Jamaica rural islanders assured me that todies sleep in their burrows at night, but I feel they do this only when incubating and brooding. I checked many holes of *T. mexicanus* and of *T. todus* and found no evidence that they were used for sleeping, resting, or shelter. However, considering the extremely rapid metabolism in todies (see Chap. 6) and the cold night temperatures at high elevations, it is conceivable that *T. angustirostris*, *T. todus*, and *T. multicolor* might spend the night in burrows either asleep or in partial torpor. It is noteworthy that Central American motmots, which do not usually sleep inside their burrows, do so when at high elevations (Skutch, 1945b).

After the young leave their nests they, too, sleep in the foliage. During two successive dusks in Luquillo rainforest (27 and 28 April 1969), adults led a newly fledged bird up to sleep in the inner twiglets of the subcanopy (see Chap. 11). In contrast to some wrens and swallows, todies never take their young back to the burrows, either for sleep or shelter. Motmots and kingfishers also abandon the burrows after the nesting season, which suggests that this may a typical coraciiform behavior.

Observations on all species of *Todus* indicate that they retire at dusk (as late as 19:12, June, *T. mexicanus*) and arise during early dawn (as early as 05:17, March, *T. subulatus*).

Wing–flicking

Todies rapidly and repeatedly flick their wings. Probably originating as stretching or flight intention movements, Wing–flicking is an important accompaniment to Preening and Bathing. Often during periods of very active feeding todies rapidly dart around, repeatedly flicking their wings like some warblers and bananaquits (pers. obser.). When immobilizing food todies may Head-shake and Wing-flick.

Wing-flicking is especially conspicuous in the non-Puerto Rican species, both during foraging as well as in agonistic and courting behavior (see Chaps. 5 and 8).

5
TERRITORIALITY

Of the hundreds of todies of all five species from which I gathered data on territoriality, the most information was obtained from about 40 pairs of *T. mexicanus* in Luquillo Forest.

It should be borne in mind that todies are not social; they never flock or nest socially. The only occasion when I encountered more than two adults at one time was during territorial aggression. The statement that todies "line up on telegraph wires like swifts, on the lookout for insects" (Dorst, 1967: 37) is erroneous.

Pairing

To learn whether todies remain paired throughout the year or separate after the breeding season, whenever I located a tody I observed it sufficiently long to determine if it was solitary or paired. The results are summarized in Figure 5.1, and may be interpreted as follows. Todies generally remain paired through the year, although the bonds are loose in the nonbreeding season. From February to June, the months of extensive reproductive behavior, an average of 70% of the todies are paired. The drop in observed

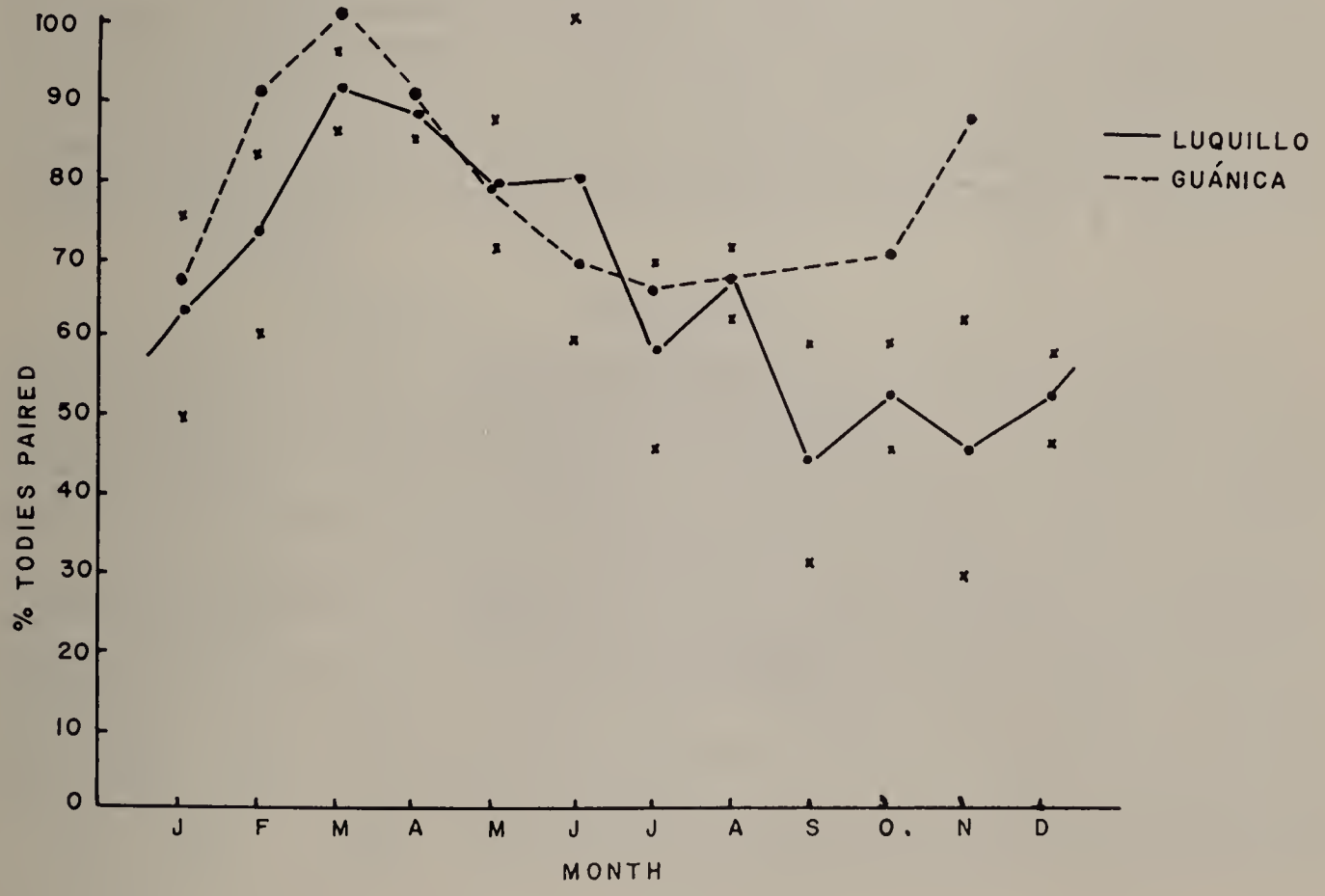


Fig. 5.1 Pairing in *T. Mexicanus* in rainforest and arid scrub. Data are from approximately 2,000 hours of observation from September 1968 to September 1970. Means are used for rainforest data; X's represent extremes.

pairs after April is attributable to the fact that one partner is often incubating or feeding young and thus is unobserved, and also because unpaired young augment the general population.

As seen in Figure 5.1, the percentage of pairs observed at Guánica was almost always higher than at Luquillo. Even though I have no exact quantitative data, it seems that territory size at Guánica is smaller (approximately 0.5 ha) and this coupled with favorable weather increased the conspicuousness of the birds and the apparent greater frequency in occurence of pairs.

It is noteworthy that there was no month, even during extremely stormy periods, when less than 29% of the observed todies were paired. This low figure occurred during November 1968 when 440 mm of rain fell; every day was cloudy, foggy, or rainy and birds were difficult to see. In Guánica the lowest percentage of paired birds recorded was 65% (July 1969); this was when fledglings temporarily augmented the population.

Further evidence that todies remain paired throughout the year comes from the observation that todies may build fresh holes many months before use, beginning as early as September, and that given pairs remain within roughly the same home ranges from year to year.

Home Ranges

The home range of todies is larger than the breeding territory, the latter being an area centered on a suitable nesting bank which is defended vigorously in the breeding season. On many occasions I saw members of a pair forage up to 60 m beyond their breeding territory boundaries when the owners of a contiguous territory were not close by. Todies probably overlap adjacent territories to a considerable extent when foraging after the breeding season.

Territories

To determine territory size, my husband and I surveyed and marked all trails and roads at 33 m intervals. In addition, there was at the El Verde (Map 1.2) site a circular, string gridwork formerly used in ecological studies (Odum, 1970). Using these grids I pinpointed the locations of todies with reasonable accuracy. I also banded 23 todies, the small number being due to difficulties in capturing them and to high nestling and fledgling mortality. I covered the study areas as well as possible by foot, following todies, marking trees, and plotting the positions of the birds on maps. Places where two pairs moved together and interacted aggressively enabled me to determine territorial boundaries. On many occasions todies chased, Wing–rattled, or otherwise threatened in identical spots each year.

El Verde

In the 10 ha El Verde study area, territory size ranged from approximately 0.6 to 1.2 ha, and averaged 0.7 ha (1.8 acres). I found that pairs in smaller

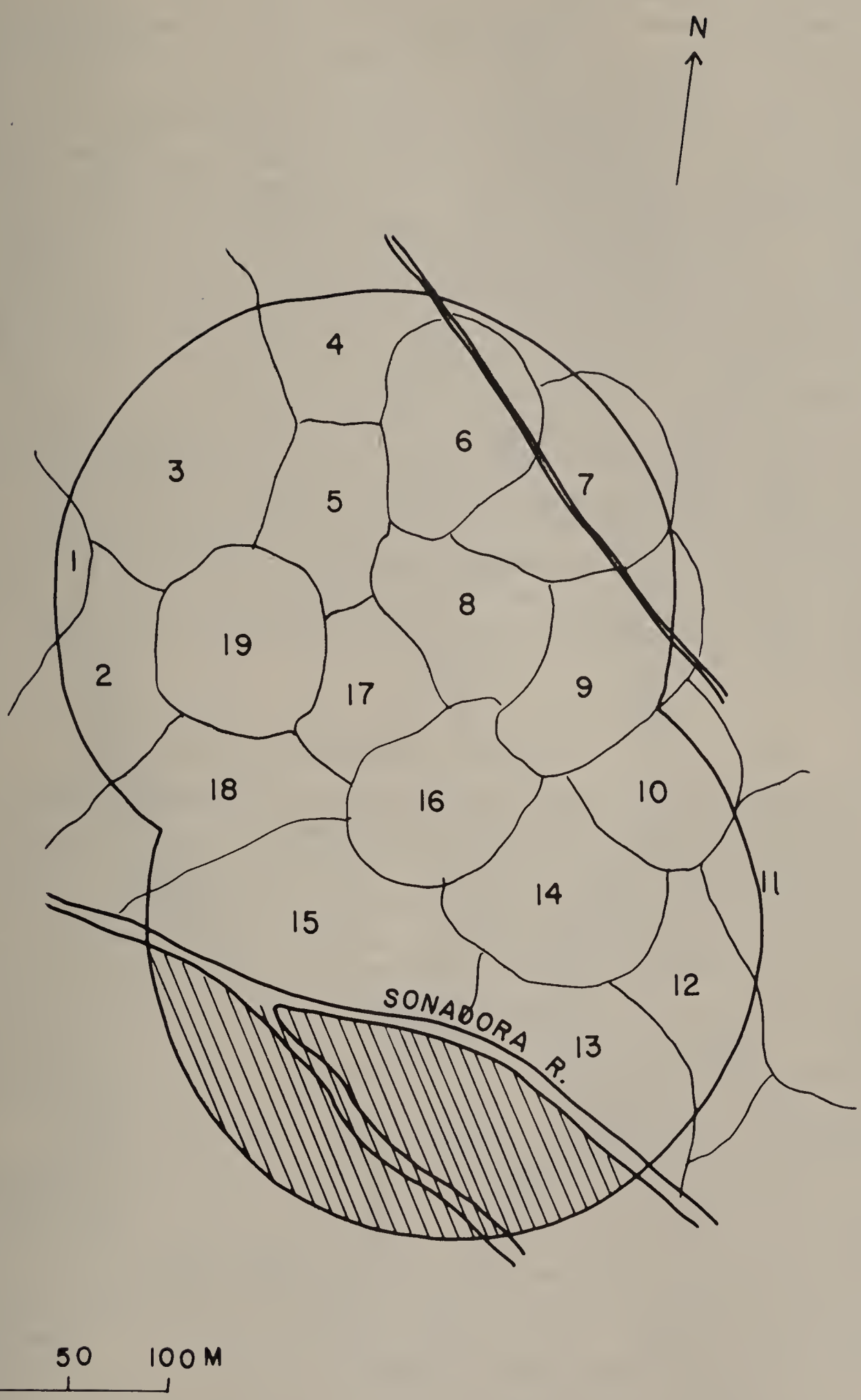


FIG. 5.2 El Verde site, showing approximate boundaries of 19 breeding territories. Average area was 0.7 ha (1.8 acres). Shading represents unstudied area.

territories defended them more often and more vigorously than those occupying larger ones. The site (Fig. 5.2) contained eight territories in their entirety and parts of 11 others. Although the territories varied in size according to subhabitats, individual territories appeared to be stable from year to year. The territories were clumped, and thus smaller, in areas with large stretches of suitable banks (pairs 6 through 12) and were largest in flat, open expanses of forest (pairs 1 through 4) and in bouldered ravines (pairs 13, 15, and 18). Large rocky rivers are generally avoided, not only because of the lack of nesting banks but probably on account of flash floods which cause the rivers to overflow frequently, eroding the adjacent ravines. Tumbling, cascading rivers are also noisy, and as tody contact calls are low-toned, birds may have difficulties in communication. I found only one successful burrow in a river bank (Chap. 7).

Using most of the same study areas, Recher (1965) estimated a tody density of nine pairs completely enclosed within the plot but not filling it, compared to my eight. Superimposing his territorial boundaries for each of four visits, I calculated that in his study area he included 12 pairs, wholly or in part, compared to my 11. The resulting approximate density is 0.7 ha (1.8 acres) per pair, the same as in my study. In addition, his largest territory was about 150 × 60 m, which is very similar in dimensions to my largest, which was 150 × 75 m.

La Mina—Mt. Britton

The approximate range of territory size at La Mina—Mt. Britton was 1-1/2 to 4 ha, and averaged 2.0 ha (4.9 acres), a range which remained remarkably stable from year to year. This 35 ha area (Fig. 1.1, Fig. 5.3) included 19 territories, 11 of which were completely within the boundaries. Todies are most dispersed in the pure stands of Sierra Palm as in those, for example, flanking the gullies through which the Mt. Britton trail winds. Even areas of stunted ridgetop vegetation support contiguous territories, but few todies reside in the scattered, open areas of low second-growth ferns and shrubs or in the steep ravines containing house-sized boulders. As at El Verde, territory size varied within the same vegetation type, depending on local geology, soils, plant cover, and canopy height.

A comparison (Table 5.1) between La Mina—Mt. Britton and El Verde, a Tabonuco zone area at a lower elevation, indicates that at higher elevations breeding territory size increases, corresponding to decreased *linear* density. Considering the third dimension, canopy height, we find that the *volume* occupied is broadly similar at both elevations but is increased slightly at the higher elevations. This is possibly because there are fewer insects and also because nest sites are limited at higher altitudes.

Recher (1965) concluded that 2.5 birds occupied his 3.6 ha plot, comparing well with my two birds per 1.5 to 4 ha, calculated from a much larger area. I found the largest territories in pure stands of Sierra Palm, similar to the composition of Recher's plot.

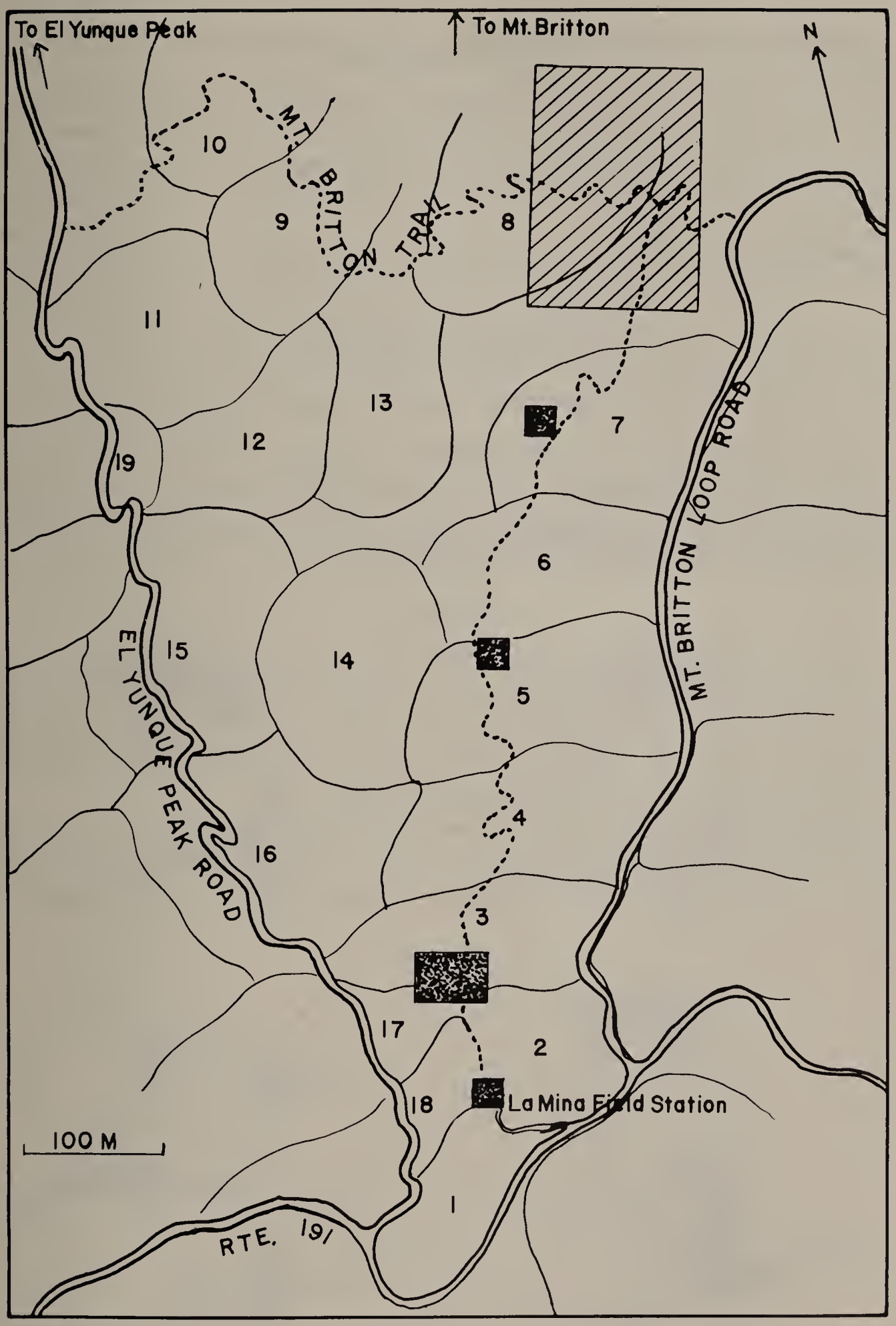


FIG. 5.3 La Mina—Mt. Britton site, showing approximate boundaries of breeding territories. Hatched rectangle is Recher's (1965) study site.

TABLE 5.1

COMPARISON OF LINEAR, AREA AND VOLUME DENSITIES OF *mexicanus* IN TABONUCO AND SIERRA PALM FORESTS, LUQUILLO FOREST

	Range & approx. mean canopy hgt(m)	Linear density per km	Breeding Territory Area(ha)	Breeding Territory Volume(m^3)
TABONUCO (El Verde)	13 - 20 (16)	0 - 25 (10.3)	0.6 - 1.2 (0.7)	92,000 - 142,000 (113,000)
SIERRA PALM (La Mina-Mt.Britton)	5 - 10 (8)	0 - 5 (2.8)	1.5 - 4 (2)	84,000 - 168,000 (136,000)

Territorial Behavior

Agonistic Displays of *T. mexicanus*

In the Puerto Rican Tody 12 displays were observed; these are discussed below in order of frequency of observation, and are compared with displays in other *Todus* species. A flow diagram (Fig. 5.9) summarizes behavior patterns associated with increasing levels of motivation.

Bobbing

One's first glimpses and memories of *T. mexicanus* are invariably of tiny, shining green, rapidly bobbing birds (Fig. 5.4), uttering loud nasal sounds quite disproportionate to their size. To effect the characteristic bob, the perched tody moves rapidly up and down, stretching its legs and body to its fullest extent, then quickly relaxing them.

Any nearby disturbance, such as intruding todies, people, cars, or airplanes, immediately causes the bird to bob rapidly. When potential predators are close, or parents are "urging" their nestlings to fledge, Bobbing and its

Fig. 5.4 Bobbing in *T. mexicanus*.

accompanying vocalizations (Beep-trill, Bee-beep, accelerated Beep; see Chap. 3) reach almost frenzied heights.

Males, probably the only sex that Loud Beeps, bob more frequently than females, as Loud Beeps are typically accompanied by high bobs. Bobbing increases the apparent size of the bird and appears to be important during territorial skirmishes, when todies fluff and bob at an accelerated pace. This behavior may be analogous to Flank Displays in the other species of todies, none of which bobs, except for *T. multicolor* which does so occasionally.

Sometimes todies bob silently after landing from a feeding maneuver, during nest excavation, or while waiting to enter a hole.

Even before young fledglings have gained sufficient strength to stand high on their perches they attempt Bobbing, which I saw as early as the first day out of the nest (age 19 to 20 days). From age 27 days on the birds bob frequently.

Crest–raising and Fluffing

Fluffing is common in many animals, especially when they are motivated to attack. Todies raise their crest feathers to varying degrees, spread their

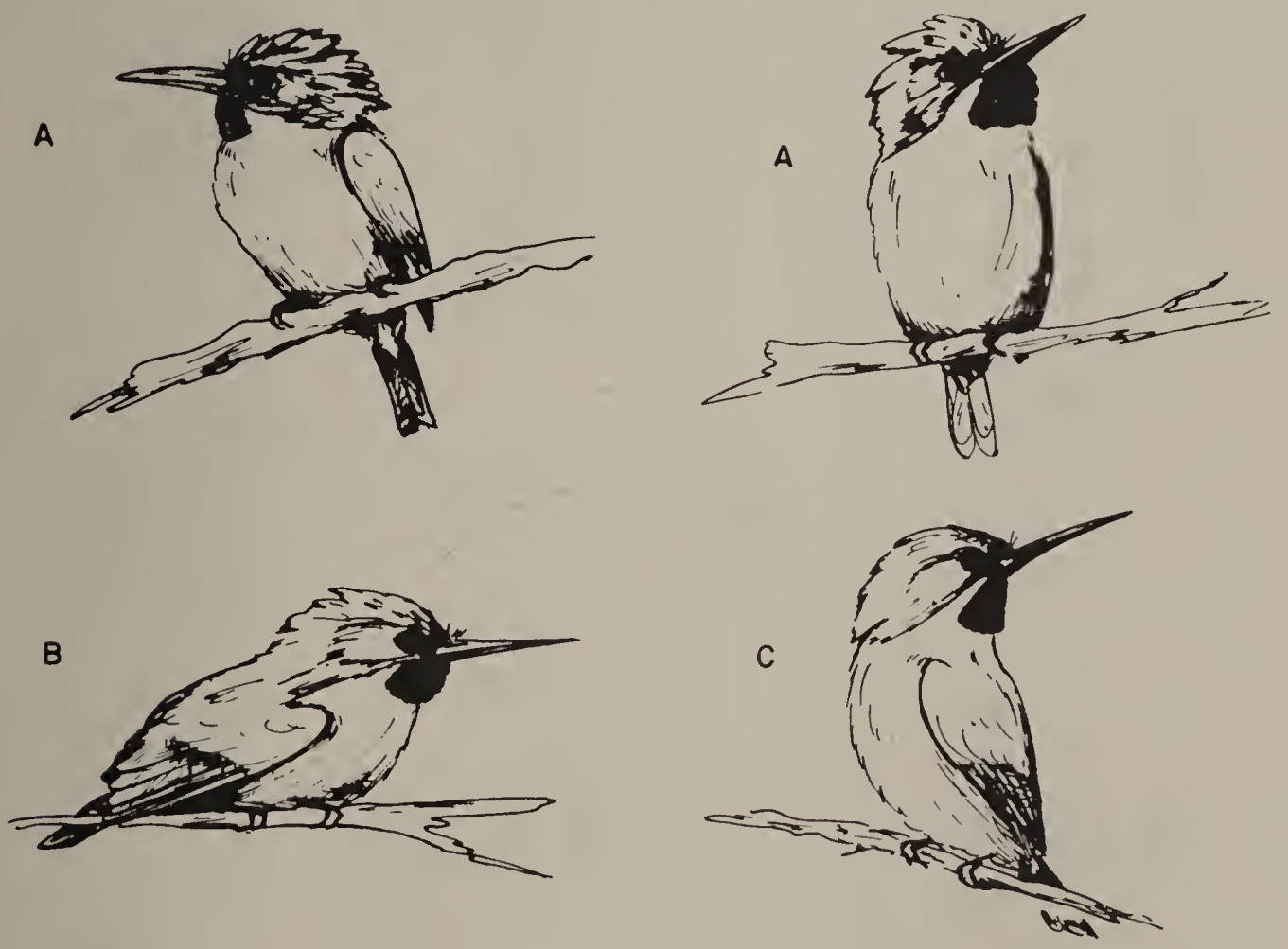


FIG. 5.5 Agonistic postures in *T. mexicanus*.
A. Crest-raising and Fluffing. Typical posture; this species rarely proceeds further than fluffing its crest.
B. Horizontal Fluff and Glare.
C. Face-away.

TABLE 5.2

RELATION BETWEEN FLANK COLOR AND DISPLAYS

SPECIES	NO. STUDIED FIELD	NO. STUDIED SKINS	AMOUNT OF PINK[1)]	DESCRIPTION OF FLANKS	BRIEF ACCOUNT OF FLANK DISPLAY
T. subulatus	69 pr (5 pr displaying)	83	2.8	Large pink flanks, expanded greatly during display, some pink on breast and belly	Most striking of all species. Puffs out breast, side, flank and undertail feathers to a remarkable degree, extending them over total wingedge, obscuring primaries and some secondaries. Pulls wings far into back center and constantly wing-flicks upwards, to 2 cm vertically above dorsum. Tufts of pink project outwards from lower body, especially noticeable from rear. Crest, gorget and mantle feathers expanded.
T. multicolor	30 pr (5 pr displaying)	82	2.1	Large patches, virtually confined to flanks	Like *subulatus*, but no Wing-flicking or high intensity displays seen (observations in the non-breeding season).
T. angustirostris	32 pr (3 pr displaying)	26	1.0	Pink confined to flanks. Little normally seen, but many hidden feathers expanded during display	Similar to above but less striking. Less pink appears and Wing-flicking although constant, never reaches a height of 2 cm above dorsum. Less gorget puffing.
T. todus	91 pr (9 pr displaying)	27	0.5	Very little pink normally exposed on flanks, but expanded during displays	Even less conspicuous than *angustirostris*. Yellow, green and pink flank feathers expanded over lower wing edge. Much Wing-flicking, but rarely more than 0.5 cm above dorsum.
T. mexicanus	many hundreds of prs (1 pr displaying)	104	0.0	Flanks yellow. Trace of pink in three males.	Generally no display. Fluffing of yellow flanks over wing edges seen once in three years. Occasional slight Wing-flicking.

1) Average of specimens studied, using a standard scale of 1 - 5:

1 = pink flank patch less than 2 cm
2 = pink flank patch approx 2 cm; little pink on breast
3 = pink flank patch extends to wrist; some pink on breast
4 = large pink flank and side patch; much pink on breast
5 = large pink flank and side patch; much on breast and belly

breast feathers and erect the remainder of their contour feathers, appearing at times like round balls of fluff.

T. mexicanus seldom fluffs all of its feathers (Fig. 5.5). On the single occasion when I observed the species completely fluffed out the flank feathers were extended over the whole wing edge, partly obscuring the primaries and secondaries. This occured during an aggressive display toward an intruder at a nest at which three adults appeared to be feeding young. A slate-irised individual (probably male) maintained this fluffed position for 4 min, several times pulling his wings far back, shaking his body vigorously, and refluffing before engaging in short darting chases and Wing–rattling with the intruding "male."

This behavior appears to be a vestige of the striking Flank Displays of the other *Todus* species (Fig. 5.10; Table 5.2).

Chasing and Supplanting Attacks

These are basic elements of territorial delineation in all species of *Todus* which lead to stronger forms of ritualized combat. Often the rivals briefly touch as they chase vigorously; at other times they pass very close before veering sideways. When chasing or supplanting one another todies fly with almost hummingbird-like speed; often it is impossible to observe whether or not they touch. In either case the movements are stereotyped; I saw

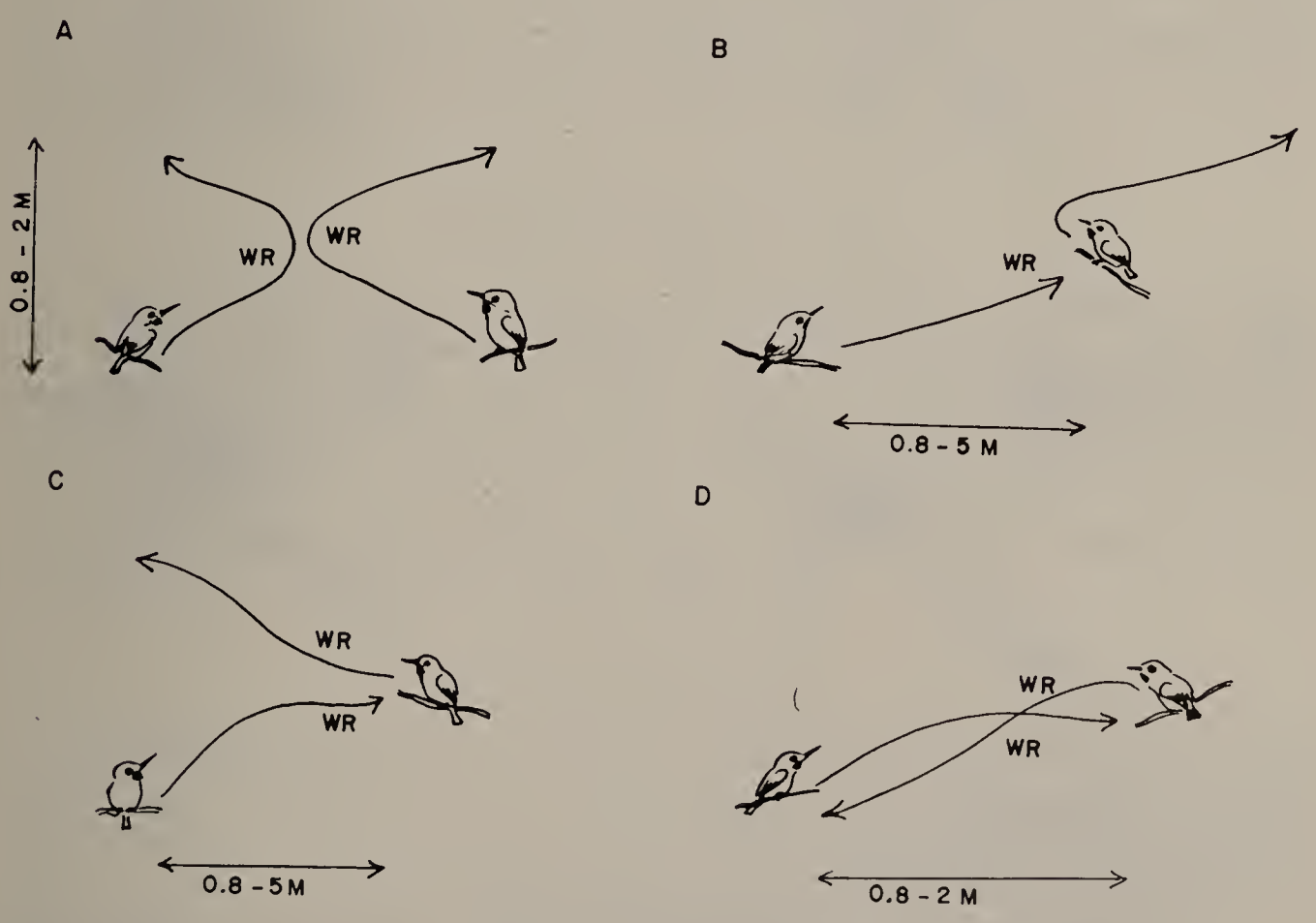


FIG. 5.6 Typical flight paths in Chases (A and D), Supplanting Attacks (B and C), and Perch-swapping (D).

todies in actual combat on only three occasions (see Bill–fencing and Aerial Tumbling).

Aggressive displays are very similar to courtship displays, as they are in many animals. If tody females did not adopt submissive postures, or if I could not discern the iris color of the two participating birds, or if I was unsure of the motivation behind the behavior, I could not be certain whether I was observing aggression or courtship.

Chasing (Fig. 5.6) may be effected without Wing–rattling, a behavior seen many hundreds of times. As the tendency to attack increases, the birds speed up their short flights (generally 0.8 to 2 m, but up to 5 m) and Wing–rattle with greater intensity until a manakin-like crack is produced.

Supplanting attacks, performed by one or both sexes, accompany Chasing and Wing–rattling. The bird with the higher relative tendency to attack pursues the other, which flies and is replaced on or near its perch by the attacker (Fig. 5.6B and C). Sometimes todies swap places by switching perches (Fig. 5.6D).

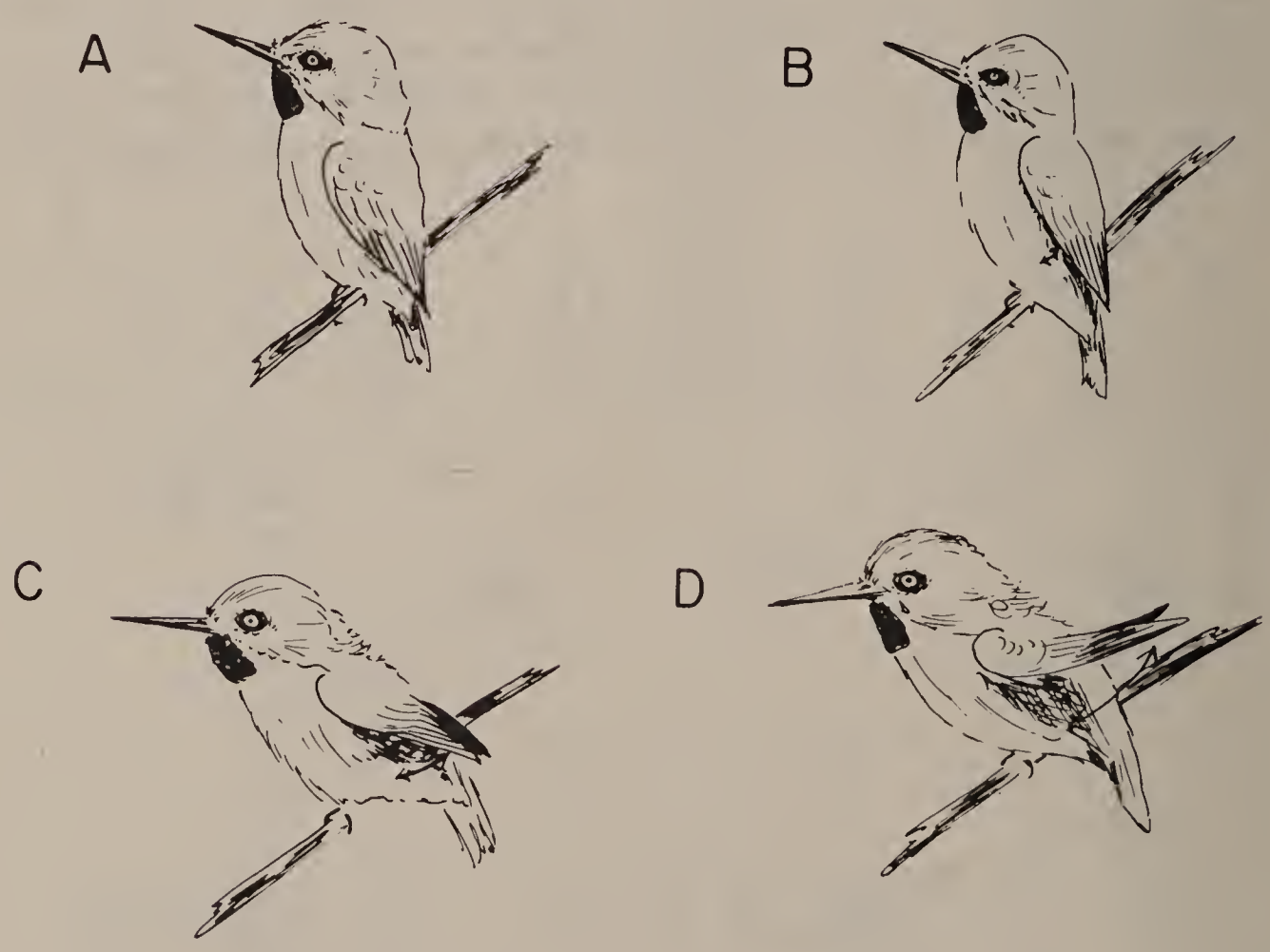


FIG. 5.7 Wing-flicking.

A. Normal resting position.
B. Slight outward movement, typical of all species.
C. Upward and outward wing movements up to 1 cm above the dorsum, typical of *T. subulatus, T. angustirostris,* and *T. todus.*
D. Greatly exaggerated Wing-flicking, seen in *T. subulatus* during highly aggressive encounters. Wings reach approximately 2 cm above the back.

TERRITORIALITY

Wing–rattling

Of 2,027 *individual* Wing–rattles that I categorized during this study, 74% occurred during hostile encounters. In addition, of 430 Wing–rattling *bouts*, lasting from 1 sec (1 Wing–rattle) to 27 min (85 Wing–rattles), 70% were involved in defense. From two to six todies, usually three or four, participated in these encounters, which were usually at the territorial boundaries of two pairs of birds. (For additional details see Chap. 3.)

In addition to Wing–rattling, I encountered six bouts of Throat–rattling (52 rattles) in *T. todus* when a bird actively chased and displayed. Three cases involved four birds; the balance appeared to involve mated pairs. Throat–rattling (associated with Chasing, Wing–rattling and Flank Displaying) seems to be agonistic, but it may have a courtship function.

Wing–flicking

Todies rapidly and repeatedly flick their wings away from and back toward their bodies, opening them slightly on the outward thrusts (Fig. 5.7). It is a commonly observed year–round behavior in todies, which is particularly conspicuous in the non-Puerto Rican species, where it has been elaborated and incorporated into agonistic and courtship displays (Chap. 4, 6).

When the bird is foraging the movement is barely perceptible, as it is given from an upright position, and the wings are moved mostly laterally (Fig. 5.7B). When todies are aggressively or sexually motivated the direction, speed, and degree of the wing movement is greatly exaggerated (see later under Flank Displays). It is possible that predominatly *vertical* Wing–flicking indicates aggression and *horizontal* Wing–flicking indicates courtship and submission (Chap. 8); more data are needed to verify this.

Horizontal Fluff and Glare

In this display the tody assumes a horizontal position, leaning forward, and puffing out its feathers, especially those of the breast, scapulars, back, and flanks, and appears larger (Fig. 5.5B). Its bill is held horizontally; periodically the bird raises its crest, staring intently and motionlessly at its opponent, which occasionally Faces Away.

I observed this posture only once in *T. mexicanus* but several times in *T. angustirostris, T. subulatus,* and *T. todus.*

Face-away Posture

This posture is present in most birds and mammals, signifying a certain degree of submission. In it the tody perches normally, somewhat fluffed, and from time to time twists its head almost 180° to face in the opposite direction (Fig. 5.5C). The aggressor during this time leans forward in the Horizontal Fluff position and glares, as has been described above.

The behavior was seen several times during high-intensity agonistic bouts in *T. mexicanus,* but not in the other species. It is likely that a very high

state of motivation is necessary for its appearance. I saw no Gaping, a behavior commonly associated with Facing-away postures in other birds, such as gulls and thrushes.

Aerial Flights and Tumbles

As agonistic motivation intensifies, simple chases become more elaborate as todies pursue one another over longer distances, weaving irregular paths, circles, and semicircles among branches and foliage (Fig. 5.8). These chases, sometimes quite graceful, were seen on 10 occasions in *T. mexicanus*. They are usually preceded and followed by short rapid darts and accompanied by loud Wing–rattles. The flights cover a distance of up to 16 m, which is the longest flight seen in *T. mexicanus*. They occur near roads or clearings, and are performed from 2 m up to canopy level above the ground.

After one series of chases 8 m in the air, two males from adjacent territories vigorously clutched each other and dropped 3 to 4 m. On another occasion as an intruder (probably a helper) was flying toward an occupied nest, the owner sped after it and grasped its body; both then turned about 40° and flew 6 m across the road still clinging together. I did not observe this behavior in other species, but it probably occurs on rare occasions as it has been described in *T. subulatus* by Cory (1885).

Upright Sleek and Upsidedown Positions

Two rival Puerto Rican Todies assumed these unusual postures while sitting for a moment side by side after the highest-intensity bout of aggression

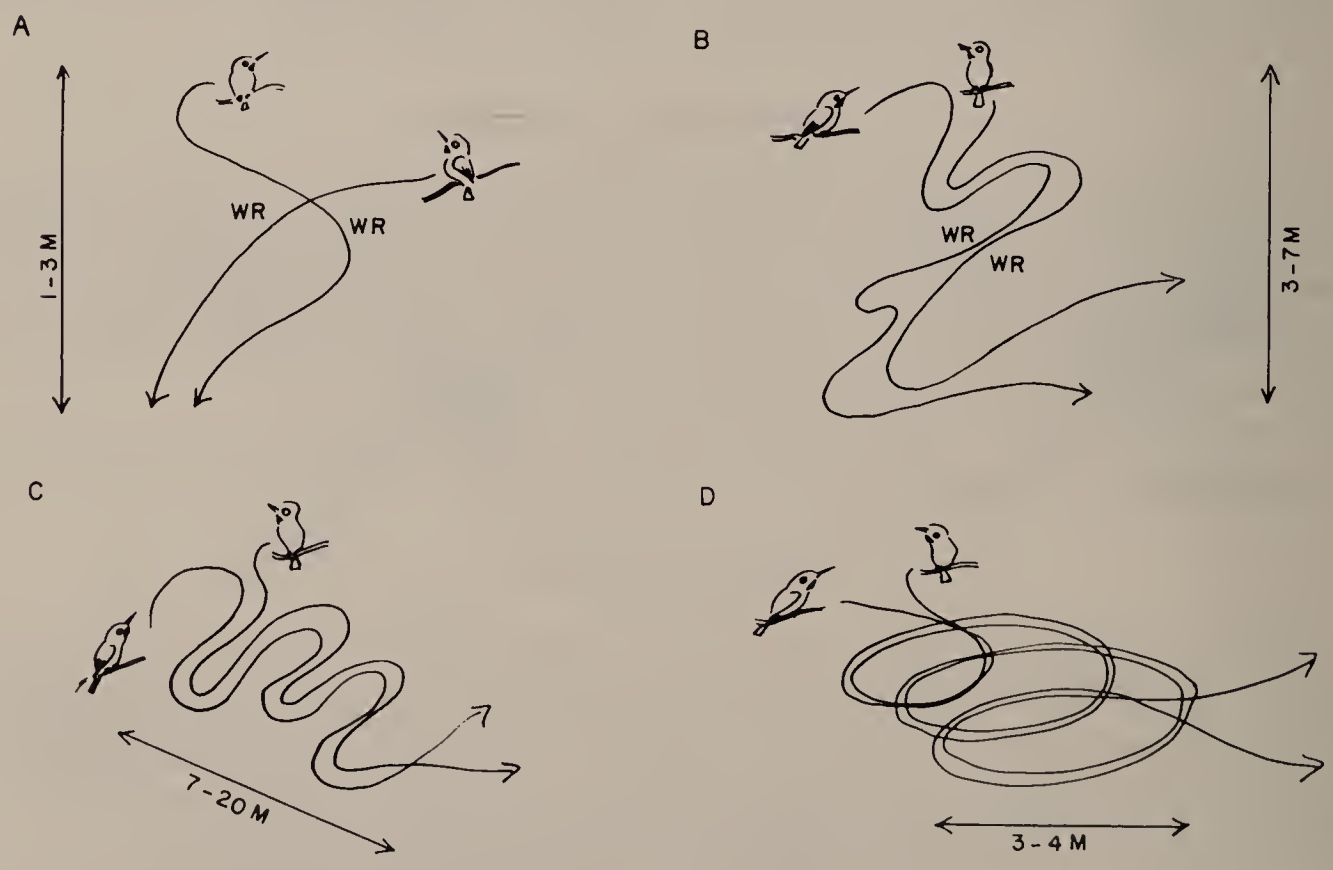


FIG. 5.8 Patterns of chases and aerial flights in *T. mexicanus*.

I observed. Six adults were Chasing and aerially displaying, Wing–cracking, and vocalizing noisily, when two birds (sexes?) chased one another and landed on a sturdy twig. One assumed an Upsidedown position, while the other perched adjacent in an Upright Sleek position. Both had unruffled plumage, straight bodies, and vertically-pointing bills. After 3 sec the Upsidedown tody returned to a normal Upright posture. Both birds then Fluffed and Bill–fenced (see below) for several seconds before resuming energetic Chasing and Wing–rattling.

This behavior was noted on an April morning four days after the surviving fledgling of a brood of three had emerged from a nearby nest where two helpers had greatly assisted in feeding the chicks. These helpers also fed the surviving chick for two days after its emergence. Although none of the birds in the aggressive bout were banded, it is very possible that the two parents, the two helpers, and two birds from the adjacent territory were among the participants.

Neither this nor the following display was seen in the other species, although Daniel (1902) reports a "bittern posture" in the Cuban Tody.

Bill–fencing

I saw this behavior on the single occasion of Upright Sleek and Upsidedown positions noted above. The fluffed rivals perched, fencing with their bills, and pushed each other with their bodies for several seconds.

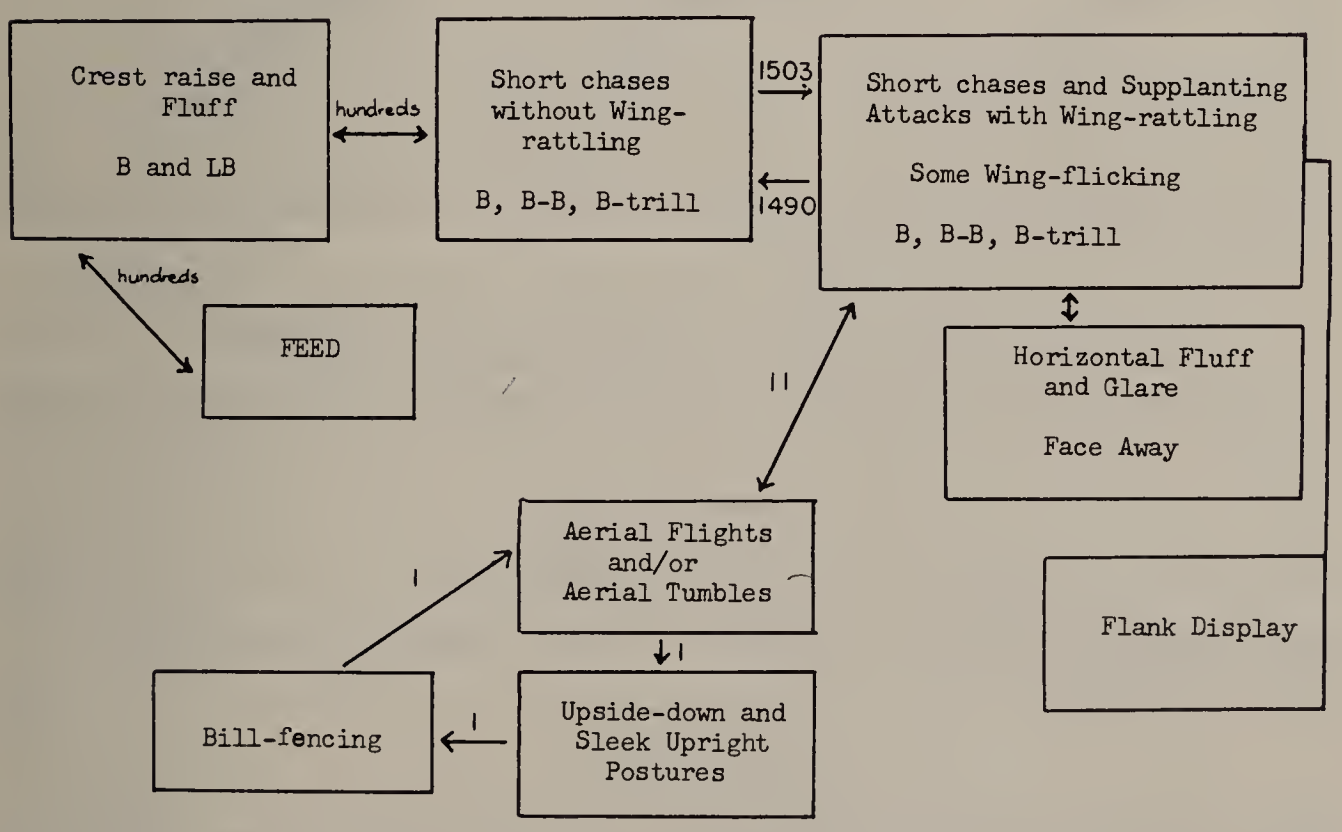


FIG. 5.9 Flow diagram representing agonistic displays in *T. mexicanus*. Read clockwise from top left for increasing levels of motivation and their associated behavior. Numerals indicate frequency of observation of given sequence.

Vocalizations

The sounds accompanying aggression in the Puerto Rican Tody are Loud Beep, Bee-beep, and Beep-trill, interspersed with regular Beeps which are often sharp and accelerated (see Chap. 3). During intense excitement, they are loud and rapid, accompanied by high, fast Bobbing. In brief, typically the Loud Beep is the first signal of aggression when an intruder enters of male's territory. As the owner Bobs and Loud Beeps, the alien male responds and usually flies back to his own domain, but if not, a chase ensues, which may lead to further hostility involving the displays discussed above and outlined in Figure 5.9.

Flank Displays of Other Species

These displays (Fig. 5.10), exposing bright pink flank feathers, exhibited in varying degrees by the non-Puerto Rican Species, and briefly described

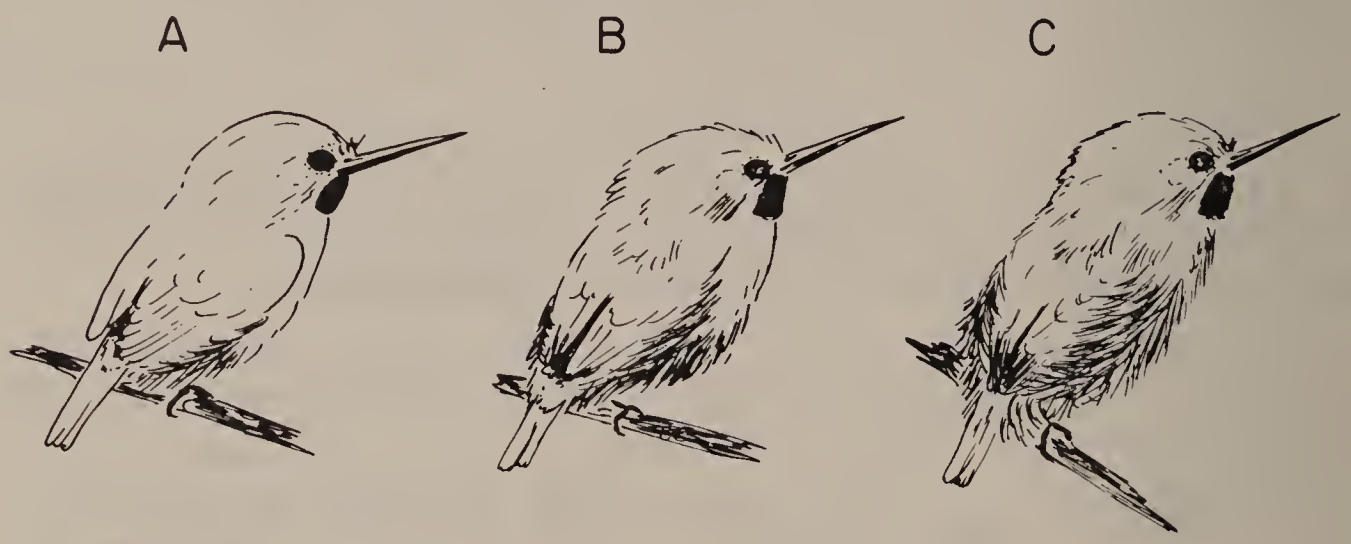


Fig. 5.10 Flank displays in *T. subulatus* (A, B, C); *T. angustirostris T. multicolor,* and *T. todus* (A, B); and *T. mexicanus* (A).

A. First stage. Body slightly fluffed, flank feathers extend barely over wing-edge.
B. Second stage. Body fluffed further, wings pulled toward dorsum, flank feathers increase in volume, crest appears and gorget becomes rounder.
C. Third stage. Whole body fluffed greatly, wings barely visible, even from rear view.

by Wetmore and Swales (1931) for *T. angustirostris,* can be conveniently divided into 4 elements, viz., Feather Fluffing, Wing–flicking, Chasing, etc., and Vocalizations.

Feather Fluffing

In low intensity displays, flank feathers are fluffed slightly. Following this the birds tightly pull their wrists dorsally, exposing fluffed flank, breast, and undertail coverts, which now extend outward and backward over the wing margins. At highest intensity the wing margins, primaries, and part

of the secondaries are invisible and the undertail coverts and lower flank feathers are further fluffed outward and downward. Scapulars, mantle, and crown feathers rise and, thus, from the rear, the tody appears as an almost circular, green ball of fluff with rosy tufts projecting laterally.

Generally todies sit upright when assuming this posture, sometimes rising up on their legs; however, prior to flights and while in the Horizontal Glare position, they lean horizontally.

Wing–flicking

Todies Wing–flick at moderate rates, accelerating to three or four flicks per second (*T. subulatus*). As their drive increases they lean further horizontally, flicking their wings vertically in an exaggerated manner. Generally the wings are 1 cm or less above the back, but one *T. subulatus* raised its wings approximately 2 cm prior to takeoff, revealing an exceptionally large patch of fluffed rosy feathers (Fig. 5.7B and C). Both lateral and vertical Tail–flicking accompany Wing–flicking during high intensity aggression.

Chasing, Supplanting Attacks, Swapping Perches, Wing–rattling, and Throat–rattling

These complete the display pattern, each appearing at different motivational levels.

Vocalizations

The predominant vocalizations (Fig. 3.1) of *T. angustirostris* are fast *chip chuis* and chattering *chippy chippy chippy chips*; *T. subulatus* utters accelerated *terps*, a trill and various guttural sounds; *T. todus* gives fast Loud Beeps and Throat–rattles, while *T. multicolor* greatly accelerates its lively whistle.

Relation Between Flank Coloration and Displays

The degree to which the flanks are extended over the wing is proportional to the number of pink feathers present. On an arbitrary one to five scale I determined the amount of pink normally exposed in each species (N = 322 skins), and related the degree of pinkness to the flank displays (Table 5.2).

The most striking display is in *T. subulatus*, which has the most pink, followed by *T. multicolor*, *angustirostris*, and *todus*, with decreasing amounts of pink.

T. mexicanus, lacking pink flanks (occasionally males have a few pink-orange feather tips, see Chaps. 1 and 15), rarely fluffs out as completely or for as long as the other species, and never flicks its wings above its body. As Bobbing is common in this species, perhaps it serves an analogous function by increasing its size during aggressive encounters.

TERRITORIALITY

Aggressive Interspecific Interactions

Todies are remarkably tolerant of other species and rarely pursue them. My observations of encounters involving Puerto Rican Todies, described in other chapters, are summarized as follows: Black–throated Blue Warblers (17), Pearly–eyed Thrashers (14), Puerto Rican Emeralds (10), Black–whiskered Vireos (10), Bananaquits (5), Redstarts (3), mongooses (2), cow and calf (2). Virtually all these pursuits were during the breeding season when the intruders approached the nest holes of todies and chased adults and/or fledglings. Todies become particularly agitated if they are prevented from entering their nests for more than 10 min; they fly low and rapidly in the underbrush, holding food in their bills, and vocalize noisily.

In addition, 436 Wing–rattles were directed toward people (mostly myself); the todies never came closer than 1.5 m.

Comparisons with Agonistic Behavior in Other Coraciiforms

There is a marked paucity of behavioral data for all coraciiform families, especially relating to hostile behavior. Skutch (1964) never saw motmots fight; kingfishers fly off or dive into the water if attacked or chased by hawks or other species (Bent, 1940). The vocal rattling of kingfishers is probably not analogous to Wing– or Throat–rattling in todies. They rattle as they fly along streams, during playful antics, and under other nonaggressive circumstances (Bent, 1940).

6
FEEDING BEHAVIOR

This chapter examines 5,203 quantitative notes on foraging behavior, plus numerous qualitative observations, among all species of *Todus*.

Methods of Analysis

With a tape recorder, notebook, and binoculars, I took detailed notes, often for more than an hour at a time, on the time, location, habitat, canopy height, the bird's foraging height, number of seconds between forays, flight length, and flight directions. I also noted whenever possible the perch's dimensions, its nature (petiole; branch; inner, center, or outer twiglets; peduncle; vine; etc.), angle, distance from the tree axis, and whether it was dead or alive.

In addition, monthly "sticky flypaper" measurements in rainforest and scrub enabled preliminary correlations of tody foraging behavior with insect composition and density.

Foraging Locations and Microhabitats

Todies are highly adaptable birds, favoring brushy areas with an abundance of branches, twigs, and leaves, but they do not inhabit open scrub or grass. The density of the preferred vegetation varies greatly. For example, in the Cordillera Central of Hispaniola *T. subulatus* occurs in almost any patch of brush, scrub, or forest that remains in steep ravines, trail borders, or pastures; I even saw it in bracken (*Pteridium aquilinum*) only 1–1 $\frac{1}{2}$ m high. But, in general, todies cannot be found where bushes or trees grow more than 3 m apart without intervening shrubby ground cover. This, apparently, is because they have short rounded wings and prefer not to fly farther than a few meters. Although not typically streamside dwellers, todies occupy gullies in lower montane areas where they occasionally capture water-loving insects, such as emerging adult mayflies and damsel flies.

T. angustirostris typically forages low in dense, impenetrable vegetation, especially when the species is sympatric with *T. subulatus*. It prefers moister, lusher vegetation than *T. subulatus* (as evidenced by its choice of ravines at lower elevations), but occasionally it inhabits xeric scrub.

In contrast, *T. subulatus* is basically desert-adapted (see Table 15.1), preferring open scrub. It forages higher in trees than *T. angustirostris* (Table 6.1; Fig. 6.4), is often exposed to the sun or sky, flies distances up to 40 m, and appears not to require an abundance of foliage and epiphytes. In all habitats it is followed with greater ease than its sister species, even where they are sympatric.

Todies feed opportunistically, capturing insects from virtually all available substrata; no given kind of vegetation is used exclusively. The principal

TABLE 6.1

FEEDING PARAMETERS SHOWING CHARACTER DISPLACEMENT IN *subulatus* AND *angustirostris*[1)]

BEHAVIOR	*subulatus* ALLOPATRY	SYMPATRY	*angustirostris* ALLOPATRY
Av flight length (m)	2.1 →	2.3	0.7 ← 0.9
Direction of feeding flights	up 90% →	100%	89% ← 83%
	down 10% →	0%	10% ← 15%
Av sitting period (sec)	15 →	30	5.3 ← 7.4
No. flights/min	3.3 →	2.0	8.0 ← 5.6
No. feedings/min	1.8 →	0.7	2.6 ← 1.2
Feeding Efficiency	53% →	37%	34% ← 22%
Av foraging hgt (m)	3.1 →	5.2	2.3 ← 2.7
Range of foraging hgts (m)	0 - 9 →	1 - 18	0.04 - 7 ← 0.04 - 6.5
Av height relative to canopy hgt	0.7 →	1.5	0.3 ← 0.7
Range of heights relative to canopy height	0.05 - 4.30 →	0.40 - 7.00	0.03 - 0.83 ← 0.13 - 4.30

1) Data are from 589 observations in allopatry and 276 in sympatry (literal), mostly in rainforest, but also in montane scrub

foraging surfaces (dead or alive), in order of preference, are as follow. (1) Leaves. These may be on terrestrial or epiphytic plants; either finely divided, long, entire, or fan-shaped and belonging to saplings, trees, undergrowth, cacti, vines, ferns, and grasses. (2) Trunks, branches, and twigs (bare or mossy). Todies forage from tree axes to outermost twiglets, but especially among inner and central twigs. (3) Air. (4) Inflorescences, fruit, and seedpods. Todies only occasionally snap insects or fruits from these. Wetmore (1916) found ambush bugs (Hemiptera, Phymatidae) in tody stomachs, and I have seen the birds swallowing flower flies (Diptera, Syrphidae), both of which are found primarily on inflorescences (see Appendix 3). (5) Ground or small sloping banks (bare or mossy). The ways

TABLE 6.2

PERCH SIZES

	DRY FOREST		WET FOREST (including *cafetales*)	
	No. observations	Av. diameter (mm)	No. observations	Av. diameter (mm)
mexicanus	170	5	500	8
subulatus	33	6	59	11
angustirostris	-	-	86	8
todus	61	5	34	10
multicolor	131	16	-	-

in which todies feed from these surfaces are discussed under Feeding Methods.

Characteristics of Perches

In order to have a view above and below them, todies choose perches (dead or alive) that are not normally covered by close–touching leaves. They alight on relatively sturdy twigs, vines, petioles, branches, palm stipes, ferns, and occasional peduncles (1–60 mm in diameter). I never saw them standing

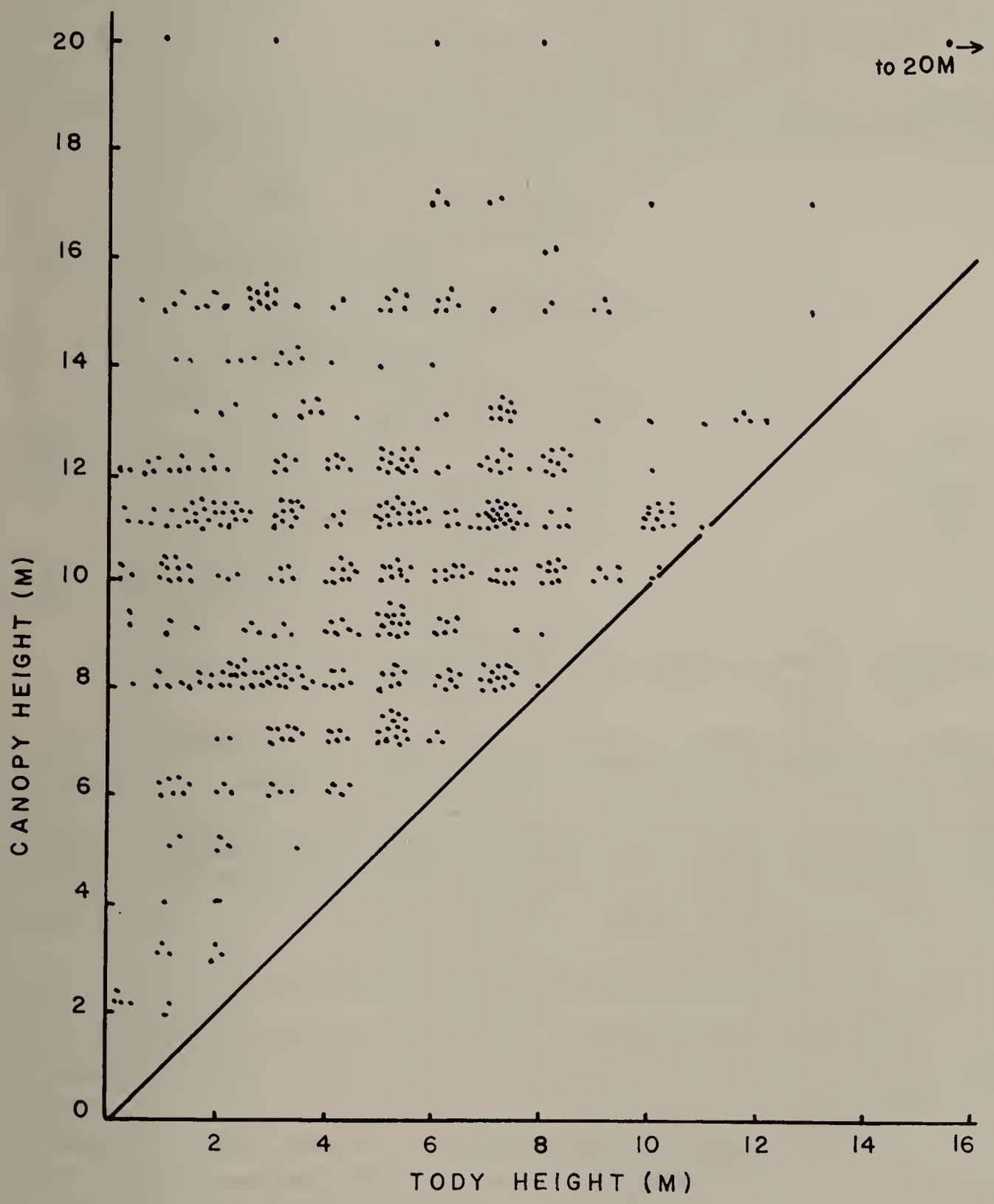


Fig. 6.1 Foraging height of *T. mexicanus* with respect to canopy height in rainforest. Each dot represents five observations (N = 2187). Average height is 4.7 m.

on leaf surfaces except palm fronds. Table 6.2 summarizes the average sizes of perches utilized by all species. Available twigs are generally smaller in dry scrub than in rainforest, which is reflected in the pattern of use.

Todies generally alight on horizontal twigs but will utilize surfaces at any inclination except fully vertical surfaces, such as tree trunks.

Foraging Height in Relation to Canopy Height

T. Mexicanus

In the rainforest this species is not restricted to any particular level, foraging from the ground to the greatest canopy height (20 m). The average height is 4.7 m ($N = 2187$), although at low canopy levels the birds tend to feed farther up in trees than when canopies are high (Fig. 6.1). However, a ground observer cannot see a tiny bird at heights greater than 11 or 12

TABLE 6.3

MEAN FORAGING HEIGHTS

	MEAN FORAGING HEIGHT (m)	
	XERIC SCRUB	RAINFOREST
angustirostris	1.7 (N=63)	2.7 in allopatry (N=148) 2.3 in sympatry (N=276)
mexicanus	2.1 (N=913)	4.7 (N=2187)
multicolor	2.6 (N=404)	
subulatus	2.3 (N=240)	5.3 in allopatry (N=49) 5.2 in sympatry (N=51)
todus	2.9 (N=326)	5.2 (N=227)
All Species	2.3 (N=1980)	4.2 (N=2938)

m; the data from 20 m canopies came from observations from a tower and my data, therefore, might be biased in favor of todies occupying levels lower than 12 m in areas with particularly tall trees. Nevertheless, when atop the tower I rarely saw todies so high; thus, although 310 (14%) observations were made in forests with canopies above 12 m, I feel that my recording error was slight. All other data indicate that todies forage in the low to middle strata of the forest (Table 6.3).

Observations of *T. mexicanus* in xeric scrub ($N = 913$) indicate that here the todies forage from ground level to 7 m with an average of 2.1 m (Fig. 6.2). As in the rainforest, they rarely forage at the full height of the canopy (9 m).

If we consider foraging heights relative to canopy height, we find that in the rainforest 50% of todies forage below the midlevel of the canopy height and 90% below three-fourths of the canopy height (Fig. 6.3). In the xeric scrub, where todies feed at conspicuously low levels, a similar pattern prevails.

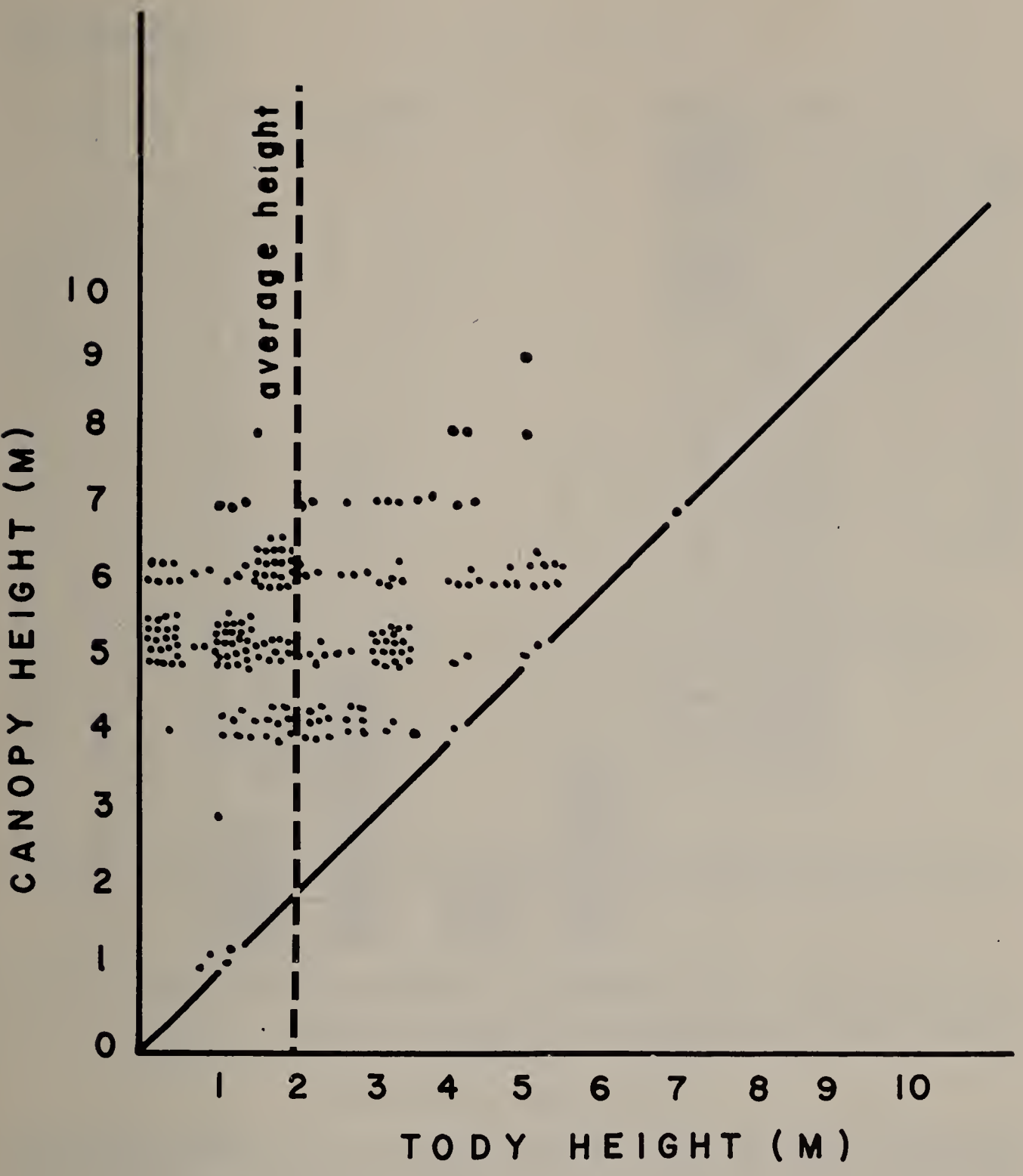


FIG. 6.2 Foraging height of *T. mexicanus* with respect to canopy height in xeric scrub. Each dot represents five observations (N = 913). Average height is 2.1 m.

T. subulatus and *T. Angustirostris*

A detailed analysis of the feeding behavior of *T. subulatus* and *T. angustirostris* reveals striking character displacement (Table 6.1). *T. subulatus* generally forages higher and less actively than *T. angustirostris*; the former feeds from 0 to 18 m (av 3.3 m) and the latter from 0.04 to 7 m (av 2.4 m), a difference which was greatly accentuated when I split the data into allopatric and sympatric components. If we consider foraging height relative to canopy height, it is evident that *T. angustirostris* feeds relatively much lower and *T. subulatus* relatively much higher than when either species

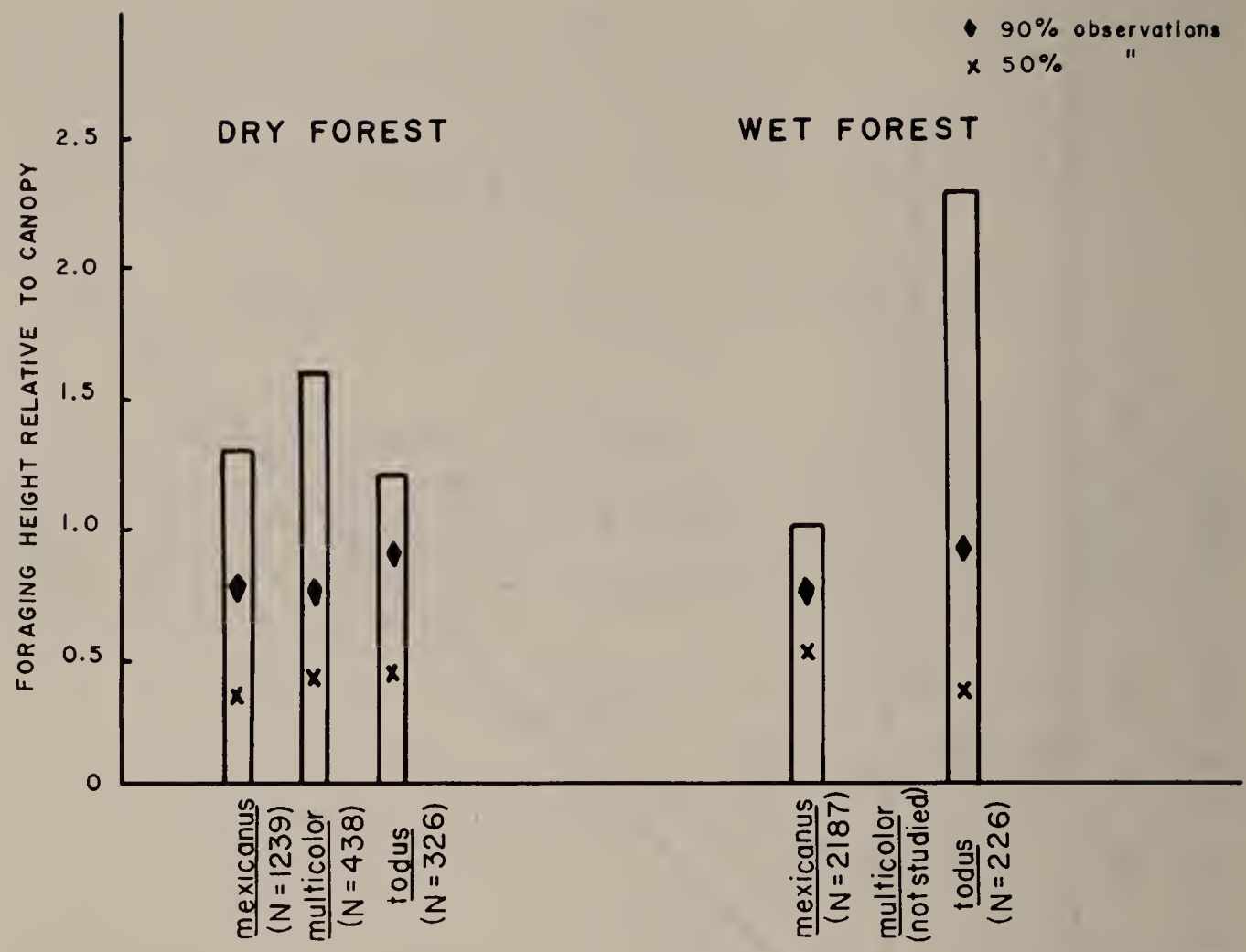


FIG. 6.3 Relative foraging heights of *T. mexicanus, T. multicolor,* and *T. todus.* Data are from wet and dry forests (N = 4416).

is alone (Fig. 6.4). This phenomenon is so striking in the field, that each species can be identified merely by its foraging height.

T. TODUS AND *T. MULTICOLOR*

Jamaican and Cuban todies forage at heights similar to those of the Puerto Rican species (Fig. 6.3; Table 6.3) in both wet and dry forests.

All todies (except the Broad-billed) spend 50% of the time foraging below half of the total height of the canopy and 90% of the time below nine-tenths of the maximum canopy height, regardless of the type of habitat. The average foraging height for the five species in dry scrub was 2.3 m, and in the rainforest, 4.2 m (Table 6.3).

FEEDING METHODS

Todies are either silent when foraging, or utter their most characteristic vocalization (contact notes). Wing-flicking is common in the two Hispaniolan species and to a certain extent in *T. todus* and *T. multicolor.* All species interrupt feeding activity to Preen, Bill-wipe, engage in agonistic encounters, or court (Chaps. 3, 4, 5, and 8).

They use two principal and four subsidiary foraging techniques. I obtained

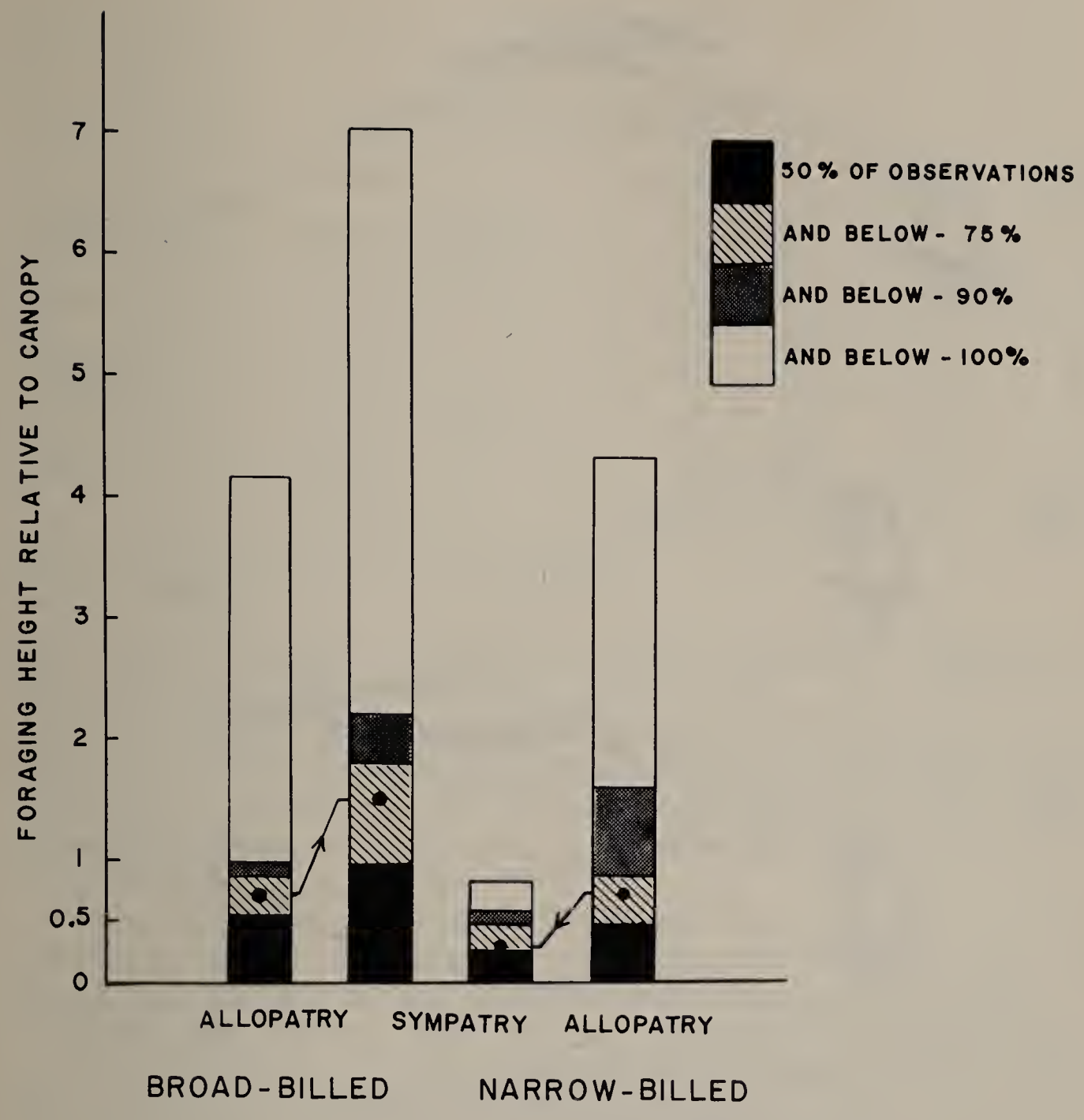


FIG. 6.4 *T. subulatus* and *T. angustirostris:* divergence in relative foraging heights when sympatric. N = 451 and 424, respectively. Data cover observations during which two species were *literally* sympatric.

the most data from *T. mexicanus* ($N = 3100$), but the other species appear to have no additional methods ($N = 1818$). The proportions of methods used differ slightly between and within species, depending on the time of the year, habitat, insect abundance, and leaf character. The development of feeding behavior in juveniles is described in Chapter 11.

LEAF-FEEDING

In this common technique (87% of the time), the bird typically sits on a perch with its bill pointing upward, at angles up to 45° from horizontal, and scans the lower surfaces of the leaves or twigs above it. It appears very alert and moves its head and eyes rapidly and jerkily. On spying an

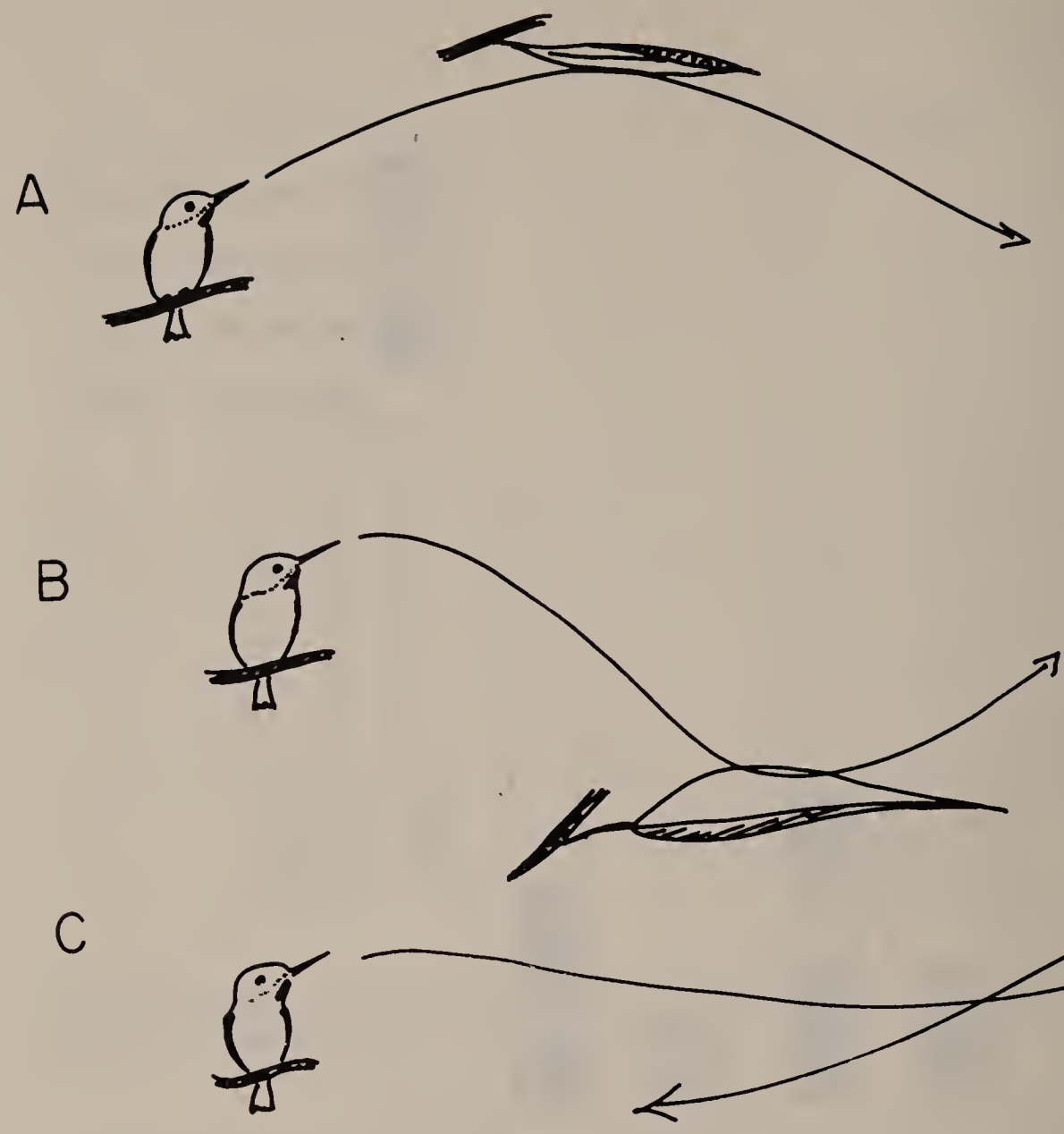


FIG. 6.5 Feeding methods.
A. Leaf-feeding from leaf undersides.
B. Leaf-feeding from leaf uppersides.
C. Air-feeding.

insect the tody flies up to the leaf or twig, snaps its bill, and continues in an unbroken arc to another perch (Fig. 6.5A). Sometimes todies spot insects from several meters away and instead of flying to them directly, fly and land for a moment on a nearer twig and then Leaf-feed. This behavior is particularly noticeable in the Cuban and Broad-billed Todies, which sit for the longest periods between forays.

Todies may feed off the tops of leaves by swooping down instead of up (Fig. 6.5B). *T. mexicanus* feeds this way most often in *cafetales* (14%) and in xeric scrub (10%). This type of feeding may depend on rainfall and insect density, as 17 (18%) of all observations in the rainforest were made from January to April, months which include a "dry" season. During wetter months insects more frequently seek shelter beneath leaves or are washed from them. During drier months, and especially in open sunny areas, insects are spotted more easily. All species fly up to feed about 90%

TABLE 6.4

LEAF - FEEDING : FLIGHT DIRECTIONS [1)]

	HABITAT	NO.FLIGHTS	UP	HORIZONTAL	DOWN
angustirostris	rainforest (sympatry)	80	89%	1%	10%
	rainforest (allopatry)	66	83%	2%	15%
mexicanus	rainforest	608	92%	3%	5%
	xeric scrub	290	89%	1%	10%
multicolor	xeric scrub	141	90%	1%	9%
subulatus	rainforest (sympatry)	16	100%	0%	0%
	xeric scrub	265	91%	1%	0%
todus	rainforest	64	91%	0%	9%
	xeric scrub	126	91%	0%	9%

1) Data are from 1656 feedings by all species

of the time, horizontally about 1%, and down about 10%, regardless of the habitat (Table 6.4).

After capturing insects todies usually swallow them while flying, but they kill larger ones by flicking their heads to and fro, or vigorously smashing their prey on twigs for up to one minute. Larger insects (up to 4 cm) are held lengthwise with their antennae projecting forward; pupae are held horizontally.

Puerto Rican Todies Leaf-fed 94.9% of the time in Luquillo ($N = 698$), whereas in Guánica they Leaf-fed only 86% of the time($N = 337$). The difference is probably because flying insects are ubiquitous at Guánica.

Despite numerous references to "favorite perches" in the literature (Fisher and Peterson 1964: 36–37; Beatty, 1931; Gosse, 1847), these are only evident during the breeding season (see Chaps. 7, 9, and 10). These perches are temporary stops before todies enter their tunnels to build, incubate, or feed chicks; they are not feeding loci.

T. mexicanus returned to its original perch in only 71 of 2,237 feeding flights (3.2%) in the rainforest, and 18 of 913 flights (2.0%) in xeric scrub. Of these 8 (9%) were double returns and 1 (0.1%) was a triple return. All other species, regardless of the habitat, returned less than 1% of the time to their original perches.

Air-Feeding

This feeding technique (Fig. 6.5C) is second in importance (8.8% of observations). The alert tody sits with its bill pointing upward and suddenly sallies up and out in flycatcher fashion to snap up a flying insect, usually returning to a different perch.

T. mexicanus feeds aerially twice as often in dry scrub as in rainforest (14% vs. 8%), reflecting a basic difference in insect abundance. Insect density is approximately twice as great in scrub than in rainforest, with particularly

TABLE 6.5

SUMMARY OF FORAGING DATA FOR *T. mexicanus*

	RAINFOREST	XERIC SCRUB	*cafetales*	TOTAL
No. flights studied	2237	913	326	3476
No. feedings studied	698	337	141	1176
Av. flight length (m)	1.3	1.4	1.1	1.3
Flight directions when both searching for food and feeding				
up	73.3%	70.0%	81.0%	73.0%
horizontal	10.2%	10.0%	4.0%	10.0%
down	16.5%	20.0%	15.0%	17.0%
Return to same perch	3.2%	2.0%	0.7%	3.0%
Importance of feeding methods				
Leaf-feeding	86.8%	86.0%	90.2%	87.0%
Air-feeding	8.0%	14.0%	5.7%	8.8%
other methods	5.2%		5.1%	4.2%
Flight directions associated with leaf-feeding				
up	91.5%	89.0%	85.0%	90.0%
horizontal	3.1%	1.0%	1.0%	2.0%
down	5.4%	10.0%	14.0%	8.0%
Flight directions associated with air-feeding				
up	81.5%	78.0%	50.0%	78.0%
horizontal	-	-	-	-
down	18.5%	22.0%	50.0%	22.0%
Av.sitting period (secs)	9.7	7.6	7.7	9.0
Range of sitting and alighting periods	±0.5 - 170	±0.5 - 123	±0.5 - 65	±0.5 - 170
Feeding efficiency (% flights resulting in captures)	30%	37%	41%	33%
Data using short intervals				
No. flights / min	3.4	4.6	4.8	
No. feedings / min	0.84	1.80	2.00	
Feeding efficiency	24.6%	40.0%	41.0%	
Months in which feeding observations taken	all year	Jan,Feb,Mar June,Nov	Feb,Nov	

large numbers of small flying Diptera in scrub (Kepler and Kepler, in prep.). This is indicated both by the types of insects caught on our flypapers and the numbers of flycatching birds that each forest supports. The xeric scrub is inhabited by three diurnal flycatchers (Gray Kingbird, *Tyrannus dominicensis*; Puerto Rican Flycatcher, *Myiarchus antillarum*; and Lesser Antillean Pewee, *Contopus latirostris*) as well as by two insectivorous nocturnal birds (Puerto Rican Whip-poor-will, *Caprimulgus noctitherus*; migrant West Indian Nighthawk, *Chordeiles minor*). The rainforest supports no resident flycatchers or goatsuckers. Bats inhabit both areas, but of the five species in Luquillo only one, *Brachyphylla cavernum*, is insectivorous and it is the least common species. This bat is abundant in Guánica. In addition, todies feed faster

and with greatest efficiency in xeric scrub, indicating a more readily available food supply (Table 6.5; Fig. 6.8).

We may only generalize about this feeding method on the other Greater Antillean islands. In Jamaica up to six species of flycatchers inhabit xeric scrub and there are usually only two in the rainforest. Turner (pers. comm. to Lack) states that in Jamaica insect density is greatest in scrub. This seems to be true elsewhere as well, at least in the tropics (Orians, 1969; Kepler and Kepler, in prep.). Therefore, as would be expected, todies living in xeric areas feed by flycatching more than they do when in wet forests. The relative rates are 14% to 3.7% in *T. mexicanus,* 2.3% to 0% in *T. todus,* and 1% to 0% in *T. subulatus.* The figures for *T. mexicanus,* taken over 2-1/2 years, are the most reliable. *T. angustirostris,* inhabiting thick undergrowth in wet forests, rarely Air-feeds (less than 0.4% of observations).

Todies habitually fly upward to feed aerially (70% to 80% of observations). This is mostly in short, shallow, parabolic paths and never in high vertical sweeps as in kingbirds.

Minor Feeding Methods

Hovering

Todies sometimes hover with upward-tilted bills like hummingbirds. This is done while in front of nesting banks or while foraging from dangling roots, juvenile ferns, leaf tips, grasses, or twigs.

Tree Trunk Snapping

Todies occasionally fly to bare or mossy tree trunks to capture crawling insects. I recorded this behavior only six times (0.5% of all observations of *T. mexicanus.* Some of the ants found in tody stomachs (Wetmore, 1916) may have been eaten in this way.

Sidling

On two occasions *T. angustirostris* hopped actively along branches, leaned over, and gleaned from the tops of leaves, similar to the actions of typical warblers. I have never seen adult todies glean by stretching up and picking insects from higher leaves, to hang upside down, to cling to leaves, or to assume any unstable body position.

Feeding Flocks

Even though territorial, todies sometimes temporarily join interspecific feeding flocks passing through their territories. They increase or initiate vocalizing as the noisy aggregations approach.

We studied 50 mixed feeding flocks in Luquillo Forest from October 1969 to October 1970 (Kepler and Kepler, in prep.), of which 24 (48%) contained todies. Flocks were small; those including todies averaged 6.1 species (4–11) and 18.4 individuals (5–51). Puerto Rican Tanagers (*Nesospingus*

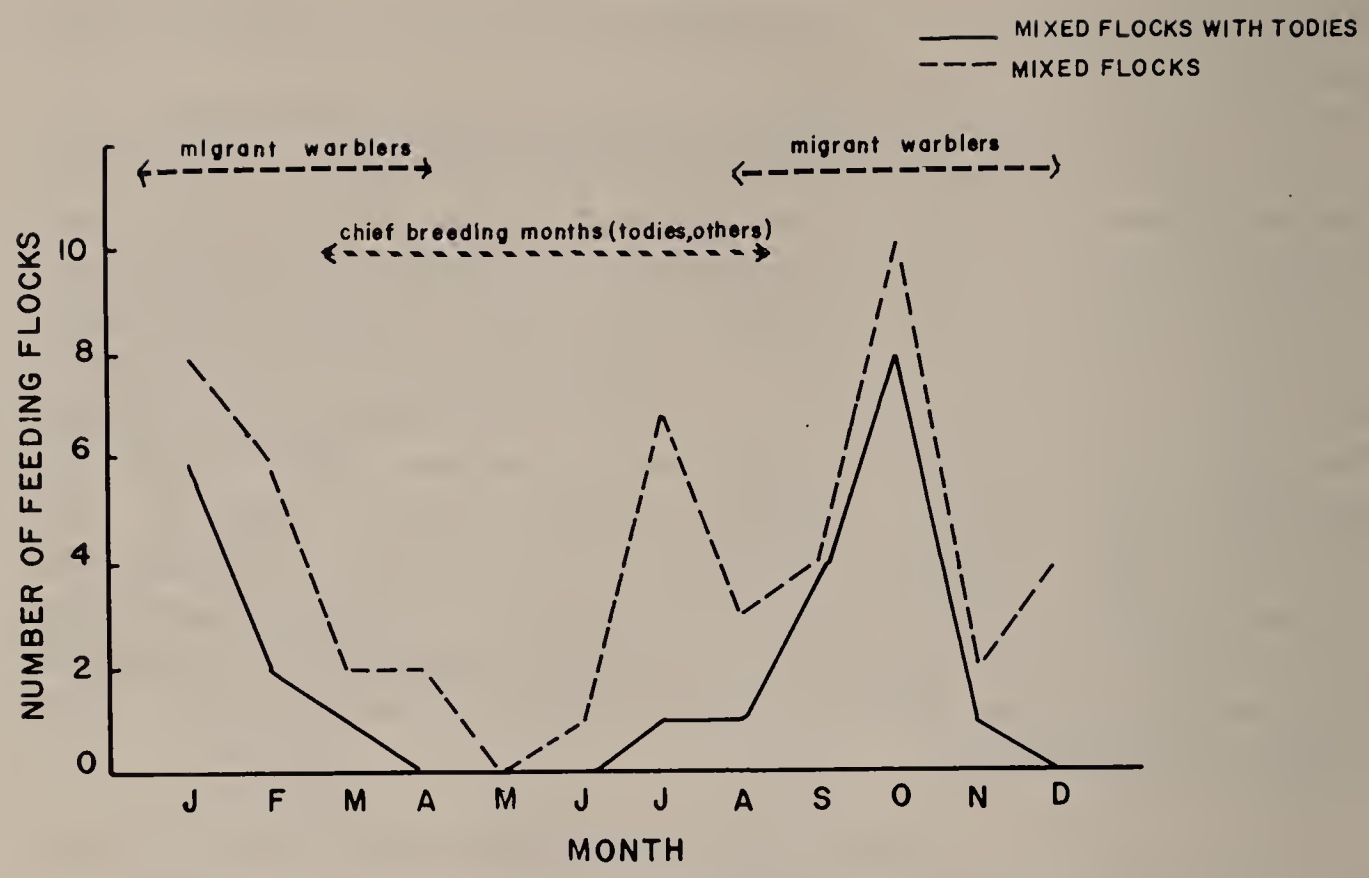


FIG. 6.6 Monthly distribution of feeding flocks of all species in Luquillo Forest. Data are from analysis of 50 flocks from October 1969 to October 1970.

speculiferus) were the core species for all flocks studied; Bananaquits (*Coereba flaveola*), tanagers, migrant warblers, and various other residents comprised the remaining species.

Flocks are not regularly encountered in Puerto Rico, in contrast to the continental tropics. They appear to form most often during autumn and winter when migrant warblers are in the forest. Todies are loosely paired during these months and readily join flocks for brief periods. As the breeding season approaches one encounters fewer flocks; only three small flocks contained todies from March through August (Fig. 6.6).

I found *T. multicolor* temporarily joining feeding flocks in dry scrub. The flocks included gnatcatchers, orioles, vireos, grassquits, thrushes, and woodpeckers.

Feeding Rates and Efficiency

For *T. mexicanus* I determined the feeding rates and efficiency by timing the intervals of feeding activity in all habitats and during all daylight hours throughout the year (except April). For the other species (Table 6.6) this was done in March, April, May, August, and September.

Todies must have an extremely rapid metabolic rate which would explain their spending almost the entire day (as long as 14 hrs in summer) feeding, with only short breaks for preening and/or reproductive activities.

TABLE 6.6

DATA USED TO DETERMINE FEEDING RATES AND EFFICIENCIES IN TODIES

	multicolor	*subulatus*	*angustirostris*	*todus*	*mexicanus*
No. minutes of timed observation	73.5	74.0	24.9	69.5	325.3
Total = 567.2					
No. intervals of timed observations	8	10	6	12	42
Total = 78					
Average duration of each timed interval (minutes)	9.2	7.4	4.2	5.8	7.7
Average of Total = 6.9					

Feedings per minute

Feeding rates are greatest in xeric scrub, averaging 1.7 feedings per minute (all species), and are slowest in rainforest, averaging 1.0 feedings per minute (four species). It is noteworthy that Gosse (1847) kept a Jamaican Tody in a room for over a day; it fed constantly, capturing approximately one

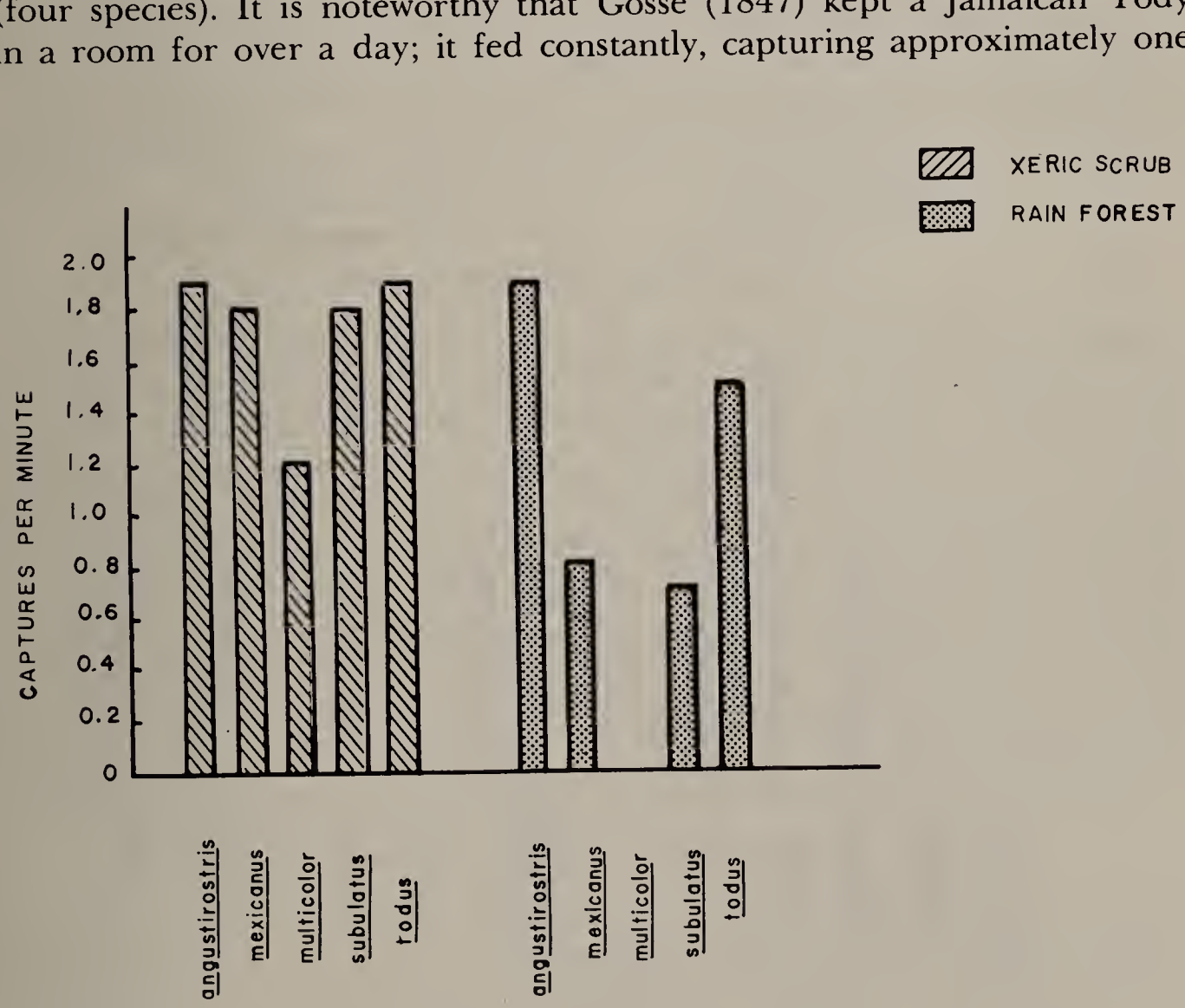


Fig. 6.7 Feeding rates. N = 670. Average rate in scrub is 1.7 feedings/min and in rainforest is 1.0 feedings/min. (Figures are high in *T. todus*, as I took most notes during the morning hours; they were spread throughout the day in other species.)

insect every minute. *T. angustirostris* is exceptional in that it feeds faster in rainforest than other todies (Fig. 6.7), but is no more efficient (see below).

Feeding Efficiency

I determined the feeding efficiency of todies (number of feedings versus number of flights) both by using timed intervals of observation and by using data on the total number of flights and feedings, regardless of the elapsed time. For example, using the former method, *T. mexicanus* flew 577 times in 325.3 minutes, capturing food 142 times. Thus it fed on 25% of its flights, giving it a 25% efficiency. Similarly, *T. mexicanus* fed on 656 of 2,187 flights, a 30% efficiency. As todies are constantly searching for food, virtually every flight not involving Chasing can be considered a feeding flight.

Feeding efficiencies are remarkably uniform in all species, regardless of habitat, differences in sitting periods, number of flights, and number of feedings per minute (Fig. 6.8). However, todies feed consistently faster in dry scrub than in rainforest, averaging 41% (roughly one capture every

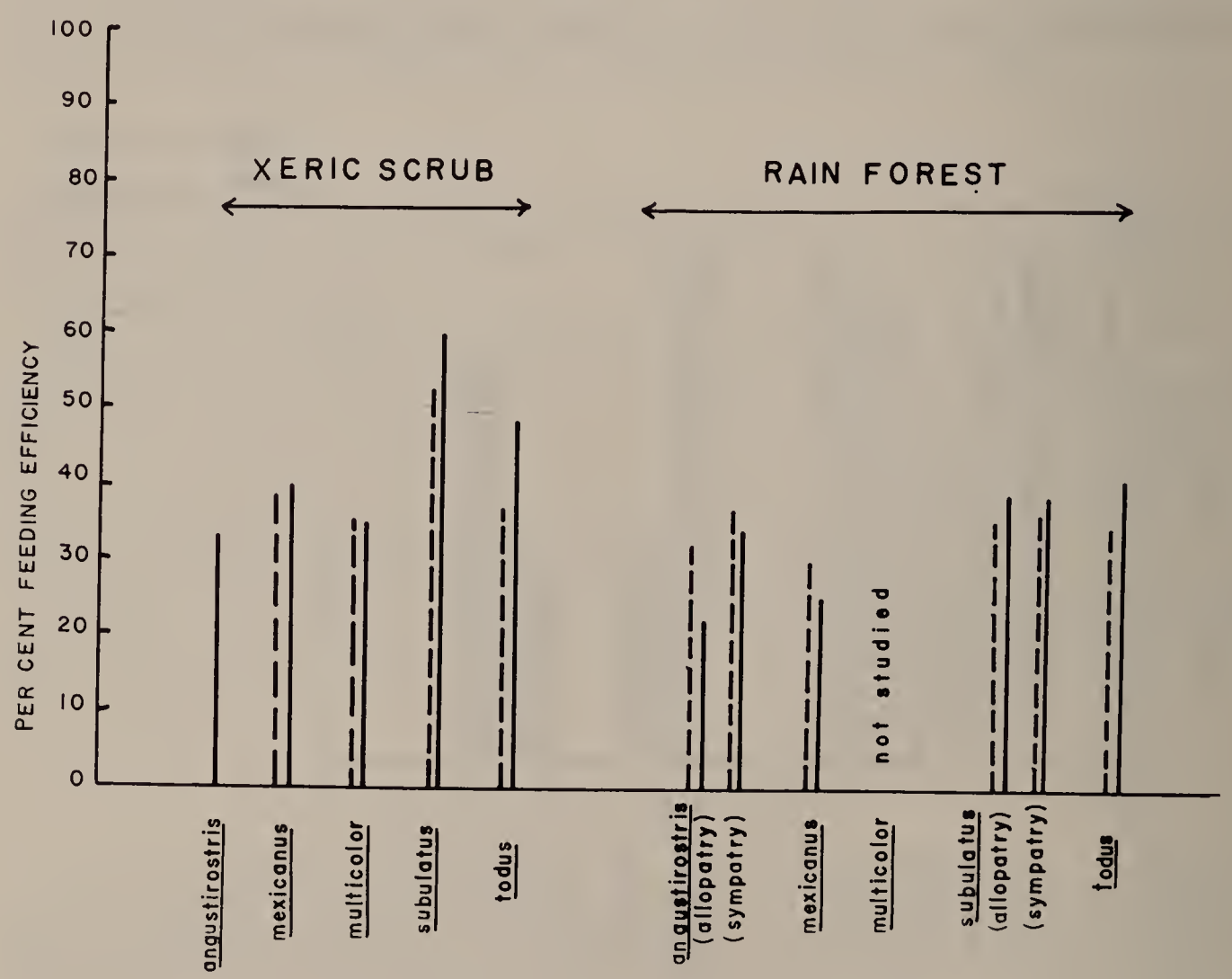


FIG. 6.8 Feeding efficiencies. Data are from scrub and wet forests. The dotted lines indicate data from timed intervals; solid lines, untimed. N = 670. Average efficiency for scrub is 41% and for rainforest is 33%.

two flights) and 33% (one capture every three flights) in efficiency, respectively.

Flight Distances

Three of the five species show remarkably consistent flight distances, regardless of the habitat, insect density, or their feeding efficiency. The Hispaniolan species are more variable, with the Broad-billed Tody the most variable. In *cafetales* and when it is sympatric with the Narrow-billed Tody, it flies relatively long distances between perches (av 2.6 and 2.3 m, respectively), but when in cactaceous, xeric scrub its flights are much shorter (av 1.9 m). The Broad-billed Tody flies longer distances and the Narrow-billed shorter distances when sympatric with one another than either does when alone, illustrating one aspect of their striking behavioral divergence (Table 6.1). (For flight distances of each species and their relation to wing length, see Table 4.1.)

Unsuccessful Captures

Todies occasionally miss their mark, at which time their mandibles clack and they immediately resume the pursuit of their prey, which either flies away or falls rapidly. It is at these times when todies display their acrobatic talents, sometimes falling more than 3 m, while snapping feverishly at the insect. However, I never saw todies drop to the ground to pick up fallen prey.

Metabolic Rate and Temperature

Oniki (1974) found unusually low temperatures (36.3–39.5°C) in seven individuals of *T. mexicanus* and theorized that these may indicate a low metabolic rate, as an adaptation for subsisting on scanty or variable food supplies. However, this study seems to show that todies possess a very high metabolic rate; also, it is known that their food is plentiful (except in severe, lengthy storms). Nevertheless, it is possible that todies enter (partial?) torpidity at night to compensate for their inability to feed constantly while sleeping. In addition, the time of day, weather, and methods of capture may influence the temperature of todies. For example, they cannot survive more than one hour in mistnets (pers. obser.; Diamond and Lack, pers. comm.), and it may be that Oniki's birds were already weak by the time they were handled.

Seasonal Differences in Feeding Behavior of *T. mexicanus*

I attempted to determine seasonal differences in the feeding behavior of *T. mexicanus* by analysing the foraging methods used (Fig. 6.9), number of feedings per minute, number of flights per minute, feeding efficiency, average sitting period, and average flight distance.

Todies Air-feed mostly during the spring months when insect density is greatest and young nestlings are fed almost exclusively on tiny insects.

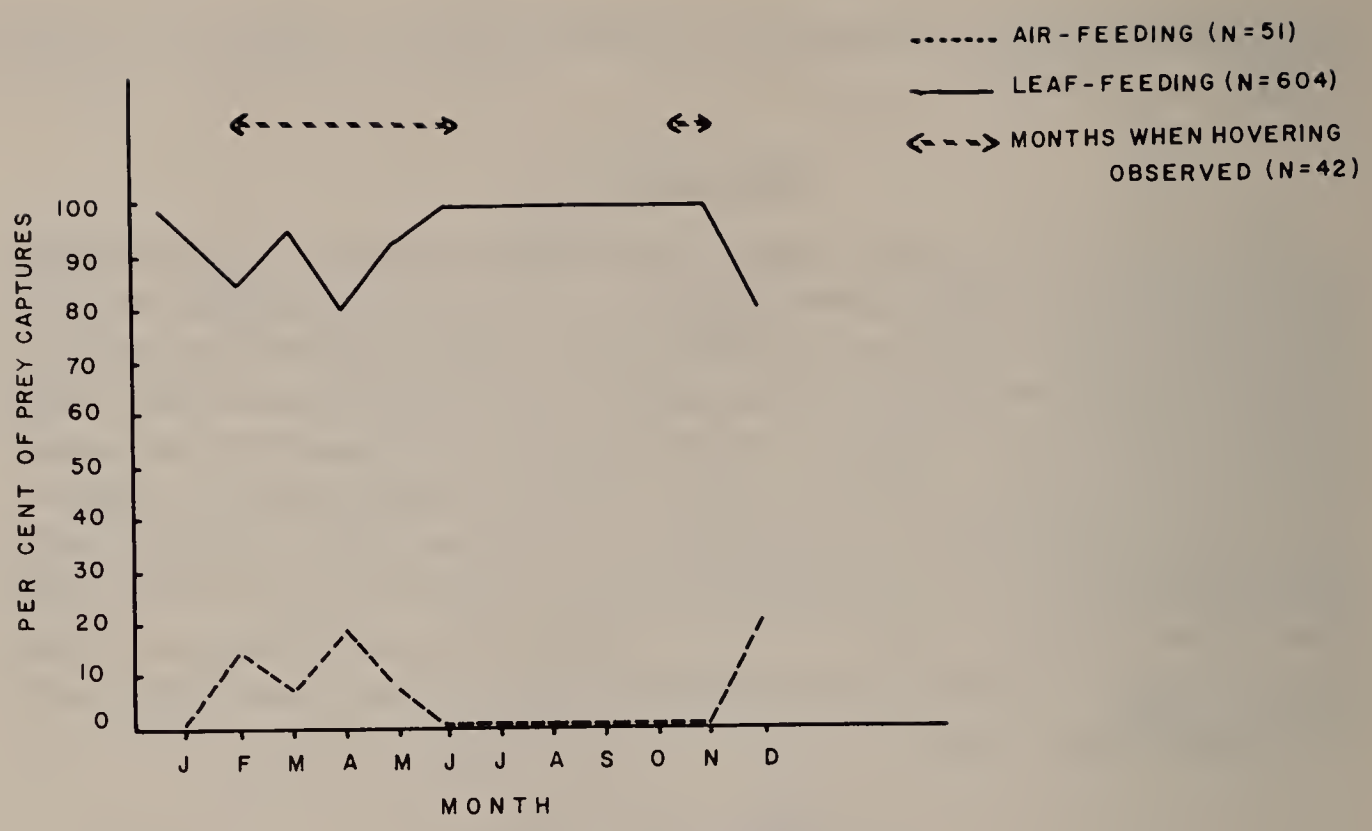


FIG. 6.9 Seasonal changes in two principal feeding methods of *T. mexicanus* in Luquillo rainforest.

During summer and autumn they only Leaf-feed; in June and July the young are fed larger insects and various types of leaf-inhabiting larvae. Fewer flying insects are available at this time (Kepler and Kepler, in prep.).

The greatest overall efficiency occurs in spring and late summer. In spring todies spend much time burrowing and defending their territories, so that when they feed they appear to do so with concentrated fervor. In late summer the fledglings, even though partially independent, still require large amounts of food from their parents; this is met by an increase in the feeding rate.

Feeding rates are lowest in the late summer; during these rainy months the todies sit longer and fly less but, as noted above, their general efficiency is high.

Feeding Differences in Scrub and Rainforest

The following are generalizations that apply to all species, but are best quantified in *T. mexicanus*. In xeric scrub, as compared to rainforest, todies: (a) Air-feed 14% of the time (cf. 8%); (b) feed faster, averaging 4.6 flights/min (cf. 3.4) and 1.8 feedings/min (cf. 0.8); (c) feed more efficiently, averaging 38% (cf. 27%); and (d) sit for shorter periods, averaging 7.6 seconds (cf. 9.7).

Food

I obtained dietary information by watching adults before they fed nestlings or fledglings and by collecting and measuring known prey. Appendix 3

TABLE 6.7

COMPARISON OF DIETS OF ADULT AND NESTLING PUERTO RICAN TODIES [1)]

ORDER	ADULTS	NESTLINGS
Diptera	30.88%	3.0%
Coleoptera	23.44%	24.7%
Dermaptera	9.4%	-
Homoptera	9.28%	30.0%
Arachnida (spiders)	8.17%	2.3%
Lepidoptera	5.21%	16.3%
Hymenoptera	4.33%	-
Lizards, insect eggs etc.	3.52%	-
Orthoptera (and Dictyoptera)	2.28%	9.5% and 2.5%
Hemiptera	1.11%	8.8%
Plant material	2.38%	-
Neuroptera	-	1.0%
Collembola (?)	-	0.7%
Trichoptera	-	0.3%
Miscellaneous	-	0.9%

1) Data from Wetmore, 1916; this study

is a compilation of all foods known to be eaten by Puerto Rican Todies from hatching through adulthood, with brief notes on other species. Table 6.7 compares diets of adults and nestlings of *T. mexicanus,* and Figures 10.7, 10.8, and 10.9 analyse nestling diets.

In summary: (1) Todies are almost exclusively insectivorous. Fourteen orders and 49 insect families have been identified. Miscellaneous foods include spiders, nematodes, millipedes, insect eggs, anoles, and fruits from six plant families. (2) Tody prey ranges from almost microscopic proportions to moths and damselflies up to 5 cm in length. (3) Principal foods are Diptera (flies), Coleoptera (beetles), Homoptera (lanternflies and leafhoppers), and Lepidoptera (moths, caterpillars, and pupae). Todies take almost anything that is available but avoid stinging wasps, bees, butterflies, and houseflies, all of which are common and sometimes locally abundant. (4) Adults show discrimination in the size and variety of foods presented to nestlings, especially during the first six days of life.

Niche Overlap in *T. mexicanus*

Todies are unique feeders; I can find no reference to any other species of bird that feeds almost exclusively from the undersides of leaves by scanning, flying up to the leaf surface, snapping an insect, and then continuing to another perch in a parabolic flight path. But one wonders if other vertebrates

use the same food source, even though they may not feed in exactly the same way.

Luquillo Forest

Birds

After estimating the relative abundance of warblers from 124 censuses made at all elevations in the forest, I analysed 698 observations of feeding by the Parula Warbler (*Parula americana*), Redstart (*Setophaga ruticilla*), and Black-throated Blue Warbler (*Dendroica caerulescens*), three migrants and possible competitors which are present from September through April. These observations are compared with those made on the Puerto Rican Tody in Table 6.8. The actual figures underestimate the true size of the warbler population, perhaps by a factor of two or three, but the relative abundance of the three species is approximately correct.

Parula Warbler.—This warbler, the second commonest in the forest, captures 35.4% of its total prey from the underside of leaves. Even though it is the least insectivorous of the three warblers, obtaining food by seven methods from leaves, twigs, petioles, inflorescences, peduncles, flowers, and berries, it probably overlaps most with the tody.

TABLE 6.8

FEEDING METHODS OF *mexicanus* AND THREE POSSIBLE COMPETITORS IN LUQUILLO FOREST [1)]

METHOD	TODY	PARULA WARBLER	REDSTART	BLACK-THROATED BLUE WARBLER
No. feeding observations	698	254	93	348
Relative abundance	10	0.2	0.2	0.4
Insects taken from leaf undersides				
Flies in arc upwards,"Leaf-feeding"	81.2%	9.4%	26.9%	13.8%
Leans up or over, gleaning from undersides of leaves, hanging upside down, clinging, or flies up and clings (Parula only)	-	26.0%	2.1%	3.8%
Insects taken from leaf uppersides				
Leans over, gleans like typical warbler	-	40.6%	37.6%	79.0%
Swoops down, grabs from upperside, continues in arc	3.4%	0.8%	6.6%	1.0%
Insects taken from air				
Flies out, catches flying insect like typical flycatcher	8.0%	-	19.4%	1.1%
Insects taken from other places				
Gleaned from flowers, buds, berries or sucked as nectar	negligable	18.5%	7.5%	1.1%

1) Data were taken from 1968 - 1971 at all elevations

FEEDING BEHAVIOR

Redstart.—This primarily insectivorous warbler is the third commonest, and feeds most consistently like todies (26.9% by Leaf-feeding), obtaining 29.0% of its prey from the undersides of leaves. It is, therefore, the tody's second possible competitor in the rainforest.

Black-throated Blue Warbler.—This is the most abundant warbler. It is 98.9% insectivorous, and is a "typical" parulid in its feeding habits. It Leaf-feeds like todies 13.8% of the time and captures an additional 17.6% of its prey from leaf undersides by various modes of gleaning. As it is present in relatively large numbers, it may compete significantly with todies.

Other Vertebrates

Anole Lizards (Anolis *spp.*; *Iguanidae*)—Anoles, which are small, diurnal, and insectivorous, are abundant in Luquillo Forest, with approximate densities of 1/sq m (10,120/ha), each eating about 34 insects per day (Lavigne, 1971).

TABLE 6.9

MICROHABITATS OF *Anolis evermanni, A. gundlachi and A. cristatellus* IN LUQUILLO FOREST [1)]

FEEDING LOCATION	% ANOLES AND TODIES RECORDED IN EACH FEEDING LOCATION		
	Anoles (Rand,1964) N = 840	Anoles (this study) N = 83	*T.mexicanus* N = 323
Trunks and contacting lianas (more than 8 cm diam)	66%	58%	0.2%
Stems (1.2 - 8 cm diam) and palm stipes	28%	36%	22%
Twigs (less than 1.2 cm diam)	1.3%	1.2%	77.8%

1) From Rand, 1964 and this study

Analysis of the structural microhabitats of three common arboreal anoles (Table 6.9) indicates that they crawl chiefly on trunks, lianas, and medium to large branches, whereas todies prefer small twigs. Anoles rarely feed from undersides of leaves and their prey overlaps only slightly with that of todies (this study; Drewry and Lavigne, pers. comm.).

Treefrogs (Eleutherodactylus *spp.; Leptodactylidae*).—Thirteen species of treefrogs occur in remarkable densities of 3/sq/m (30,000/ha) in the rainforest; nine species are sufficiently common to be considered tody competitors. In one day these frogs consume approximately 455,000 insects/ha (Lavigne, pers. comm.). One wonders whether this has an effect on the insect populations available to todies.

These frogs forage nocturnally up to canopy height, overlapping to a certain extent the prey of todies, but they do not appear to feed from the underside of leaves (this study; Drewry and Lavigne, pers. comm.)

FEEDING BEHAVIOR

Guánica Xeric Scrub

I again attempted to estimate relative densities of each possible competitor, using data from 21 censuses. Migrant warbler figures are low, as in Luquillo Forest.

Insect density is greater at Guánica than in the rainforest, but so are the numbers of potential avian competitors with todies for this resource. These include Adelaide's Warbler (*Dendroica adelaidae*), Puerto Rican Vireo (*Vireo latimeri*), Puerto Rican Flycatcher, and Lesser Antillean Pewee, in decreasing order of their abundance (Table 6.10). All these birds capture insects, a large proportion of which come from the underside of leaves, (26.3, 30.0, 40.0, and 43.7%, respectively). (Sometimes it was difficult to be certain whether the insects were crawling on under- or upperside of *twigs,* which introduces a small error into the feeding observations of all species, especially in dry scrub.)

Xeric scrub Air-feeding by the tody assumes more importance than in the rainforest. It is practiced also by the Lesser Antillean Pewee (31.3%) and Puerto Rican Flycatcher (8%). However, as indicated earlier, competition for food from this source is probably slight.

In summary, in neither rainforest nor xeric scrub do todies have leaf undersurfaces wholly to themselves. In Luquillo the Parula, Redstart, and

TABLE 6.10

FEEDING METHODS OF *mexicanus* AND FOUR POSSIBLE COMPETITORS IN XERIC SCRUB [1)]

METHOD	TODY	ADELAIDE'S WARBLER	P.R. VIREO	P.R. FLYCATCHER	LESSER ANT. PEWEE
No. feeding observations	337	262	110	50	48
Relative abundance	10	22	7	5.5	0.1
Insects taken from leaves or twigs, undersides					
Flies in arc upwards,"Leaf-feeding"	76.0%	12.6%	13.6%	40.0%	43.7%
Leans up or over, gleaning from undersides of leaves, hanging upside down, clinging	-	13.7%	16.4%	-	-
Insects taken from leaves or twigs, uppersides					
Leans over, gleans like typical warbler	-	44.0%	63.6%	12.0%	-
Swoops down, grabs from upperside, continues in arc	10.0%	0.4%	-	40.0%	20.8%
Insects taken from air					
Flies out, catches flying insect like typical flycatcher	14.0%	4.2%	-	8.0%	31.3%
Insects taken from other places					
Gleans from bird's nest airplant, ground, tree-trunk etc.	-	15.1%	6.4%	-	4.2%

1) Data were taken in almost every month of the year (1968 - 1971) in Guánica and Susua forests, at elevations up to 350 m.

Black-throated Blue Warblers overlap by 35.4%, 29.0%, and 17.6%, respectively. In Guánica, even though insect density is higher, competition from Adelaide's Warbler, Puerto Rican Vireo, Lesser Antillean Pewee, and Puerto Rican Flycatcher is correspondingly greater, these species having niche overlaps with todies of 26.3%, 30.0%, 43.7%, and 40.0%, respectively, when feeding from leaf undersurfaces (Table 6.10). Each of these species, in common with todies, also hawks insects on the wing.

Niche Overlap in Other Todies

The Greater Antilles are especially rich in examples of birds, lizards, frogs, and plants which exist as series of ecological replacements on each island. Statements about tody competitors can, therefore, probably be extended to include the species on Jamaica, Hispaniola, and Cuba, as basically similar situations are encountered there by closely related frogs, anoles, and birds, although Puerto Rico is decidedly richer in tree frogs. Limited observations of North American warblers on other islands indicate that their feeding methods, and hence degree of overlap with todies, are similar to those of the Puerto Rican migrants (this study; Lack, pers. comm.).

Ecological Counterparts

We have already discussed birds which coexist with todies, concluding that todies occupy a unique niche in the Caribbean, with very little competition from other vertebrates. But, do todies have ecological equivalents in other tropical or temperate forests or scrub? Are there other birds which utilize leaf undersurfaces to the same extent and in the same manner?

Representatives of several passerine families Leaf-feed like todies (e.g., Parulidae, Muscicapidae, Sylviidae, Paridae), but the closest equivalents are found in the Tyrannidae.

Tody-flycatchers

These small flycatchers (*Todirostrum;* 15 species), once included in the genus *Todus,* inhabit scrub, *cafetales,* wasteland, open woodland, second-growth, edge, sandy savannahs, mangrove edge, and rainforest in tropical America. Small, active, and gnatcatcher-like, with longish flat bills, they capture Diptera (Tipulidae, Tabanidae), small Coleoptera, Hemiptera, Homoptera (Membracidae), Arachnida, Hymenoptera, and other insects (Haverschmidt, 1968; Slud, 1964).

Haverschmidt (1968: 326) writes of the Spotted Tody-flycatcher (*T. maculatum*). "Like other Tody-Flycatchers it feeds by jumping to a leaf and taking an insect with an audible snap." Likewise, Skutch (1960: 475) writes of the Common Tody-flycatcher, *T. cinereum,* ". . . (they) hunt in foliage and do not make long aerial sallies in pursuit of insects. Much of their small prey is captured as they make short darts from branch to branch of some sheltering tree or bush, sometimes near the ground but often in

the tops of trees of medium size. Sometimes they fly against a leaf to pluck off an insect, and often they climb among the boughs, gathering small creatures from foliage and bark more in the manner of a warbler or vireo than of a flycatcher. They have a curious habit of hopping sideward along slender branches, wagging their narrow tail rapidly from side to side as they go."

These references generally sum up the feeding behavior of Common, Spotted, and Slaty-headed (*T. sylvia*) Tody-flycatchers, which I studied briefly in Guyana, Surinam, and Venezuela. My limited observations indicate that these species feed like *Todus* less than 50% of the time, with the Spotted Tody-flycatcher feeding more often by flying up to leaf undersides than the other two. The Tody-flycatchers are more active than *Todus* (most like *T. angustirostris*), sitting only 2 or 3 sec before flitting to another perch. Their wings are longer than todies, and they fly longer distances between feeding forays. Typically, they do not sit upright with bill pointed up searching higher leaves. Instead they hold their bodies more horizontally, like the warblers and vireos they resemble, when plucking insects from the upper surfaces of leaves. They spend much time looking downward, often swooping to snap insects off the upperside of leaves. When *T. cinereum* and *T. maculatum* are sympatric the latter appears to feed closer to the ground. Neither species feeds as rapidly as todies, even though they fly more often. Their behavior resembles that of those flycatchers which feed from foliage rather than those which hawk insects.

Tody-Tyrants and Other Tyrannids

Personal observations on the Pearly-vented Tody-Tyrant (*Idioptilon margaritaceiventis;* Venezuela), Ochre-bellied Flycatcher (*Pipromorpha oleaginea;* Trinidad and Guyana), Agile Tit-like Tyrant (*Uromyias agilis;* Colombia), Dusky-capped Flycatcher (*Myiarchus tuberculifer;* Jamaica), and Stolid Flycatcher (*Myiarchus stolidus;* Jamaica) indicate that they all occasionally Leaf-feed in addition to their regular methods of foraging. I suspect that many small flycatchers sometimes Leaf-feed like todies, especially those that are not primarily aerial hawkers.

Motmots and Jacamars

Although related to motmots, and looking like miniature jacamars, todies feed quite differently from both, although the Blue-throated Green Motmot (*Aspatha gularis*) is reported to Leaf–feed occasionally (Skutch, 1971).

My limited observations on the Blue-crowned Motmots (*Momotus momota;* Trinidad and Guyana) plus more extensive studies by Skutch (1945b, 1947, 1964, 1971) indicate that motmots sit for long periods on very sturdy branches, fly long distances as they gracefully move through the forest, and feed infrequently.

The Rufous-tailed (*Galbula ruficauda;* Trinidad and Venezuela), Paradise (*G. dea;* Surinam), Yellow-billed (*G. albirostris;* Surinam), and White-chinned (*G. tombacea;* Colombia) Jacamars which I studied all feed by working around

small areas, sitting for periods of up to 7 min before sallying out 1 m or more to capture a flying insect. Jacamars point their bills upward and move their heads jerkily but, unlike todies, have hunting perches to which they consistently return. They commonly feed near streams, capturing butterflies or dragonflies almost exclusively by Air–feeding, never by Leaf–feeding.

Summarizing, it appears that the only birds yet known that feed 25–50% of the time in a manner similar to todies are Tody-flycatchers and Redstarts.

7
BURROWS

Excavating nesting burrows in earth banks is characteristic of most Coraciiforms, a few swallows, jacamars, two parrots, a starling, a lark, some barbets, and some ovenbirds. Furthermore, an owl and some nunbirds nest in ground-level burrows. Todies, and three tiny Alcedinids (Dwarf Kingfisher, *Myioceyx lecontei;* African Pigmy Kingfisher, *Ispidina picta;* Pygmy Kingfisher, *Chloroceryle aenea*) are the smallest of these excavators, with the todies digging the shortest burrows.

The following account refers to *T. mexicanus.*

Burrow Size

The completed burrow has an almost circular entrance, averaging 3.4 cm wide (range 2.5–5.2 cm) by 3.6 cm high (range 2.5–5.1 cm). It averages 30.5 cm (range 12.4–58 cm) long in wet forests (N = 168) and is slightly shorter in dry limestone scrub (av 26.9 cm; range 12.4–38.0 cm; N = 55).

The tunnels are usually horizontal, rarely inclined up or down. In 86% of the burrows a curve (three-quarters at roughly 90°) is present, about equally divided between the right and left sides (Fig. 7.1). At the end is an enlarged, slightly depressed chamber averaging 11.3 cm long (range 8–16 cm), 9.8 cm wide (range 5–14 cm), and 6.9 cm high (range 2.5–5.1 cm) (Fig. 7.2).

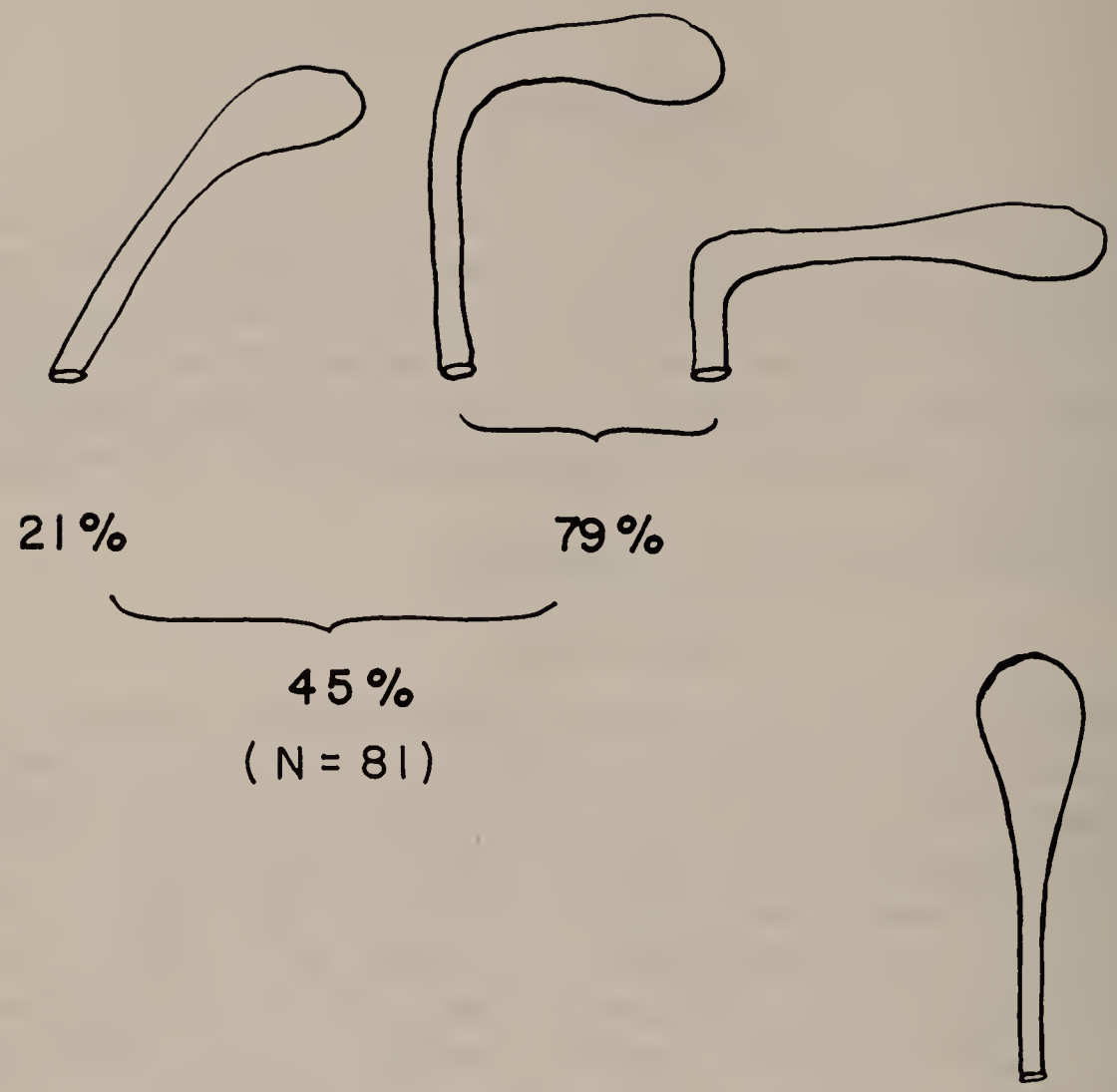
The eggs are laid in the unlined chamber on bare, compact earth which sometimes is worked into a small depression. In one nest a few small irregularly-shaped stones lay under the eggs. Coraciiforms generally do not line their nests, although some kingfishers carpet their dirt chambers with fish bones, scales, crustacean shells, leaves, pine needles, or straw (Bent, 1940; Skutch, 1957) and cuckoo-rollers use a few wood chips and dead leaves to line their nest holes in trees (Forbes-Watson, 1967).

The holes of other species of todies (N = 123) are slightly larger than that of *T. mexicanus* (Table 7.1). All rainforest todies tend to build higher above ground than those in xeric scrub (as *T. mexicanus*), but this depends upon the type of soil. In predominantly limestone habitats todies build holes in the narrow bands of soil overlying rocky outcrops. This is especially true of *T. todus* and *T. angustirostris.* The limestone of xeric Hispaniola is composed primarily of chalky, easily–excavated soil, similar to that of Guánica, Puerto Rico, and the todies, mostly *T. subulatus,* build at any height, but preferably close to ground level.

Location

Banks

All todies choose suitable banks within (Fig. 7.3) their home ranges, and during the breeding season vigorously defend territories centering on them.



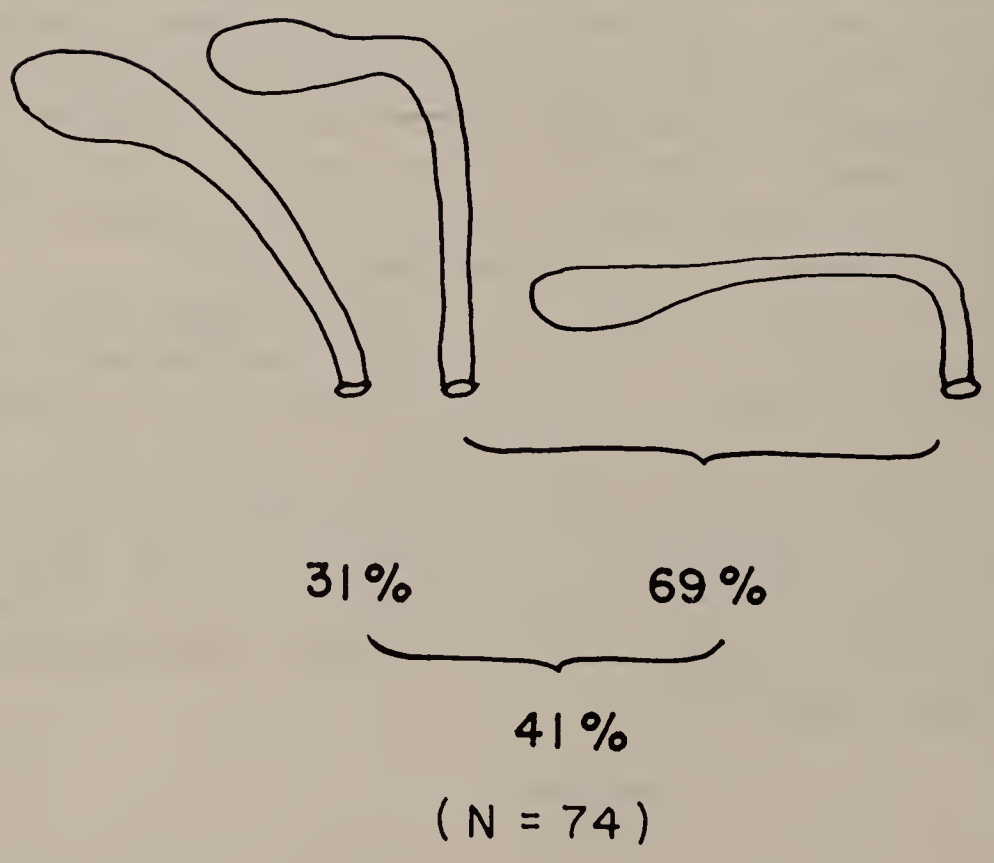


FIG. 7.1 Shapes of burrows of *T. mexicanus*.

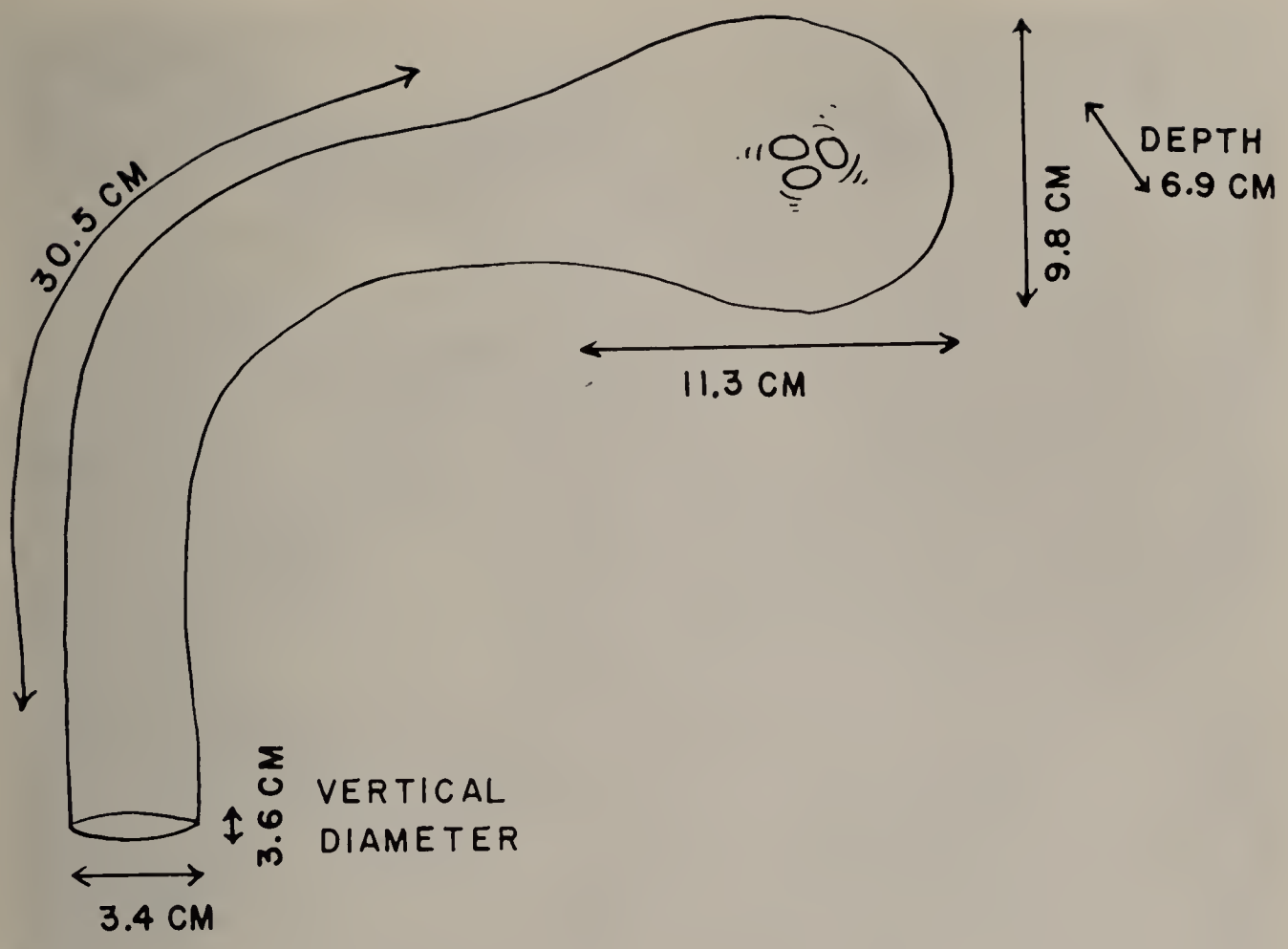


FIG. 7.2 Detail of typical nesting chamber of *T. mexicanus*.

TABLE 7.1

BURROW DIMENSIONS

	WIDTH(cm)	HEIGHT(cm)	HEIGHT ABOVE GROUND(m)	BANK HEIGHT(m)
angustirostris (N=57)	4.4	3.9	3.2	2.8
mexicanus (N=355 completed nests)	3.4	3.6	0.46 (xeric scrub)	1.1
			0.90 (rainforest)	1.6
subulatus (N=45)	3.7	4.0	1.0	1.5
todus (N=21)	3.9	3.5	1.3	1.9

1) Curves and lengths of burrows not included because data include incomplete as well as complete burrows. See text for details on *mexicanus*. Longest found was for *subulatus*, 47.3 cm, although maximum length recorded is 60.0 cm (Wetmore and Swales, 1931).

They prefer amphitheatre–shaped vertical banks, often under sheltering roots or rocks, but they will use road– or trailside cuttings, natural banks, stony and rooty soil, shallowly-sloping ground, or even a dried hoofprint of a cow (Bond, pers. comm.). In Luquillo Forest high rainfall results in frequent flash floods; since the todies nest during some of the wettest months of the year, river banks are obviously unsuitable sites, although one pair did nest early in the season in a bank 2 m above the river, finishing before the heaviest rains. In Susua Forest two of the three nests that were found were near the water; judging from my experience and reports from local

FIG. 7.3 Typical roadside nesting bank in Luquillo rainforest. Forked Ferns (*Dicranopteris pectinata, Gleichenic bifida*) provide shade. Banks are regularly sheared, providing excellent nesting banks each year.

people, it seems that at lower elevations, where rainfall is moderate, *T. mexicanus* commonly utilizes stream banks.

The banks themselves are not high. In the Puerto Rican rainforest, todies choose banks with an average height of 1.6 m, and burrowed at 0.9 m. In scrub forest, with almost twice the nesting success (94% versus 54%),

the banks are 2/3 and the holes 1/2 the height of those in the rainforest. These figures are related to predation; it appears that 0.8 m is a critical height above which mongooses either cannot smell the chick's excreta or are unable to climb the vertical slope (Chap. 14).

Amount of Vegetation on Banks

In the rainforest recently exposed bare banks offer tempting surfaces to excavate, as they are conspicuous and relatively free of hard obstacles. However, nesting success is greatest in burrows surrounded by a moderate amount of vegetation. The underlying reasons, I believe, lie in weather conditions. Most excavation occurs during the "dry season" when exposed bare soil becomes cracked and brittle, or breaks off in angular lumps. At this time 55% of the attempted burrows are abandoned. Later, on arrival of heavier rains, a further 23% of the exposed banks are partly or totally destroyed by slippage, since little or no plant stabilizing cover protects them. However, heavy rainfall seems necessary for the constant production of new banks, as the rapidly growing vegetation renders many banks unsuitable for tody burrows after 2 or 3 years (Chap. 14).

Fresh trail- and roadcuts have probably benefited tody populations in recent years (greater densities are found along trails than elsewhere; (see Chap. 2); but they are also responsible for many destroyed nests, as todies build before sufficient plant cover has stabilized the soil and protected it from drying out.

Banks laden with abundant vegetation, on the other hand, are difficult to excavate, as todies must sometimes tear away several centimeters of thick mosses and liverworts before reaching the wet, sticky soil. Todies always abandon drowned nests.

Soils

Any easily-worked compact soil is used, but moist, red clays, rich, loamy black soils, and chalky limestone "rock" produce the best results. Todies abandon their burrows readily if the soil is too rocky, sticky, etc. Other factors also lead to abandonment, such as when large chunks of earth break off, forming a lumpy tunnel subject to caving, or when the chamber becomes waterlogged.

I found one unusual *T. mexicanus* nest excavated in a rotting log of a fallen colorado tree. Salmon (1971) reported a *T. todus* nest in what was originally a woodpecker hole in a stump of bastard cedar.

In Jamaica rural islanders informed me that todies build holes in very stony banks and I saw a hole in a rocky wall where todies nested for several years. In addition, Salmon (1969) reported that while a pair of *T. todus* was excavating a marl bank, the birds carried out stones "one inch in diameter and one-half-inch thick." I never observed this behavior in any species,

but did once see an individual of *T. mexicanus* fly from a hole carrying a rather large lump of dirt.

Construction

Digging Behavior

Male and female Coraciiforms customarily build jointly; todies are no exception. In every case studied just the two adults excavated, with nest-helpers not appearing until later in the nesting cycle (see Chap. 12).

The pair arrives in the nest vicinity with a flurry but immediately reduces its noise to an almost inaudible Muttering. The birds follow each other's movements closely, Bobbing, and occasionally Wing-Whirring. (More intense Wing-rattling may indicate courtship or a territorial conflict.)

When beginning a tunnel todies behave restlessly, hovering in front of the bank, jabbing it with their long, chisel-like bills in bouts of 2–5 thrusts. Between bouts they return to nearby "favorite perches." As the hole widens they scrape out loose dirt with their small feet. At this stage there are many fine striations, made by the bird's claws, around the opening and this combined with fresh dirt at the foot of the bank identifies a new tunnel. Generally, the pair works on the burrow once or twice during the 12-minute (range 2–39 min) average stay in the vicinity of the excavation. On emerging the tody may Bill-wipe, Headshake, or Fluff. In wet weather their bills become sticky and caked with mud, and their plumage is dirty and dishevelled. They often Gape widely, toss their heads, and Regurgitate chitinous pellets. After a digging bout is completed the todies remain as a tightly-knit foraging pair.

When soil in the chamber is compacted and the burrow is in use, the passage of the adults' feet leaves two unmistakable parallel grooves on the lower side of the tunnel. Although motmots emerge tail first from their holes (Skutch, 1947), todies, except in the earliest stages of excavation when it is impossible to turn around, always emerge head first.

When in the vicinity of the nest todies remain closer to the ground than they usually do. While here they often vary their feeding methods from the typical Leaf-feeding and occasional Air-feeding, to hovering around ferns and herbs, or pulling at ground moss (see Chap. 6). They also sometimes snap up volant insects when dashing in and out of nest holes.

When a bout of digging is concluded the pair retreats from the nest area; the birds halt their Muttering and resume regular Beeping as they commence concentrated feeding. These periods away from the nest are of variable length, averaging 38 min (range 1–78 min). However, on several occasions I left after two hours without seeing them return. On rainy or cloudy days, or in the afternoon, burrow excavation may cease or be irregular; the pattern is unpredictable.

Territorial Behavior Around The Nest

Todies defend their nesting territories from trespassing birds, people, and mongooses by displays involving Wing-rattling, Loud-Beeps, and various

threat postures (see Chap. 5). Interestingly, some species do not bother them. I often saw Puerto Rican Emeralds (*Chlorostilbon maugeus*) feeding as close as 1 m above a tody hole undergoing excavation without being attacked, and Crested Anoles (*Anolis cristatellus*) regularly displayed unmolested as near as 40 cm from perched todies, who were obviously aware of their presence.

Duration

Todies begin digging as early as September (although the very early holes are never used), continuing through June (Figs. 7.4 and 7.5).

As the excavation phase lasts nine months, building is highly irregular. For 22 nests the average time to finish a nest was seven to eight weeks (range 3–17 weeks), corresponding to a growth rate of about 0.5 cm/day. One tody pair labored 12 weeks to finish a burrow only to have it destroyed by a mongoose, but constructed another nest, complete with two eggs, in less than one week!

The completed burrows are left for an average of four weeks before

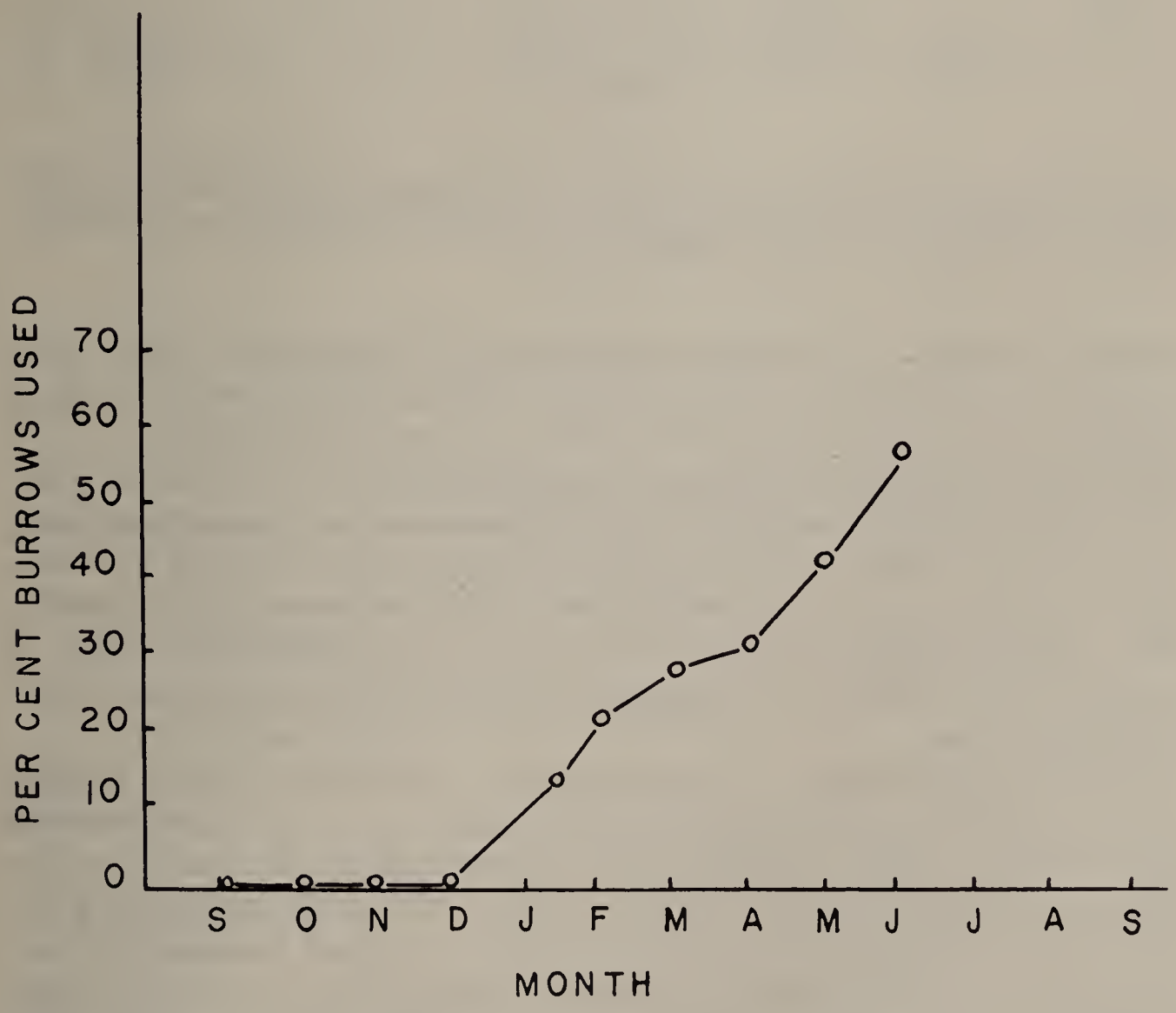


Fig. 7.4 Increase in burrow use by *T. mexicanus* with advance of breeding season in rainforest (1968–1969) season. N = 247.

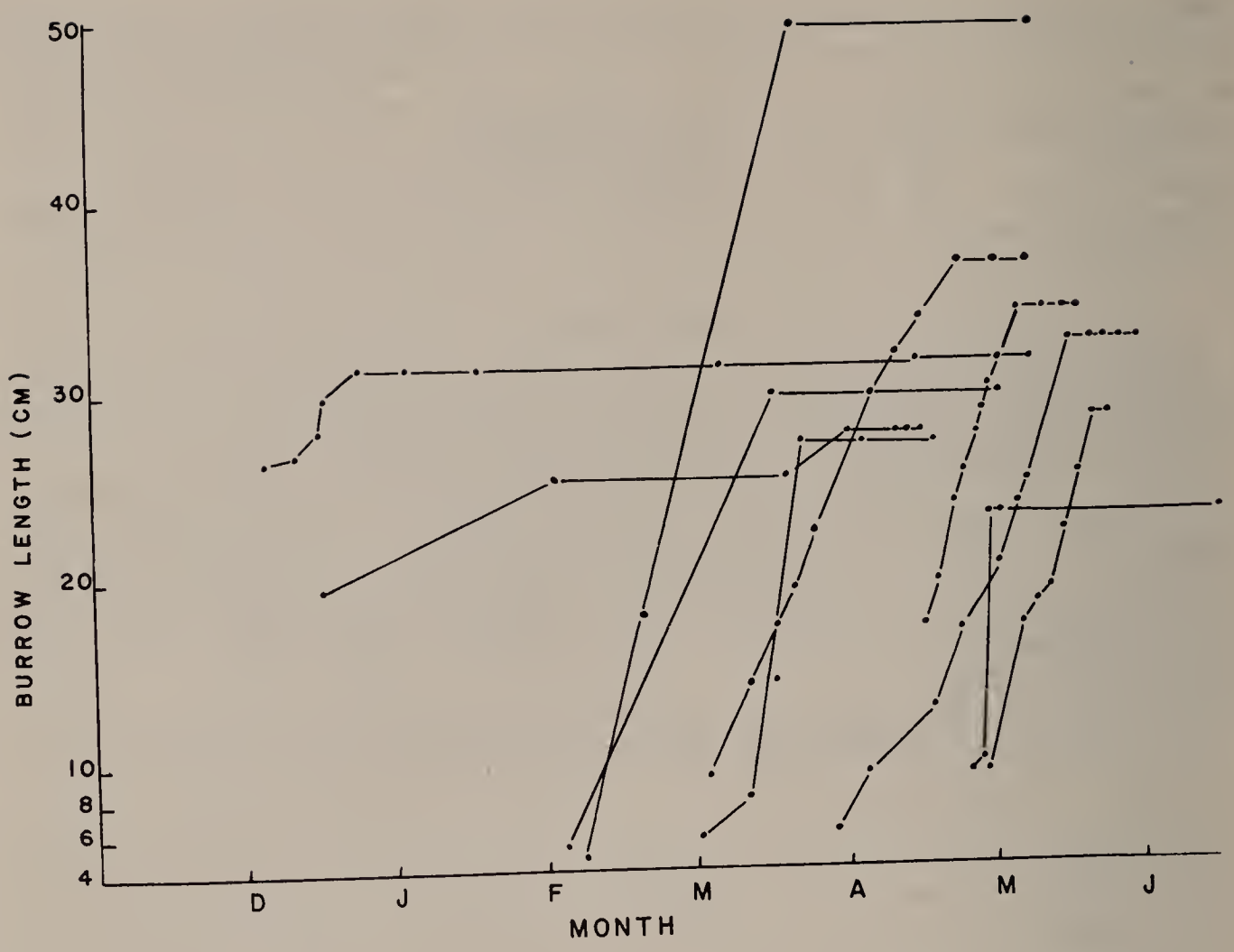


FIG. 7.5 Growth of 10 burrows continually worked on by *T. mexicanus* in Luquillo rainforest (1969–1970). Each dot represents one observation date; after completion, each nest was studied for additional data.

occupancy (range 1–17 weeks), although part of this time may be used to compact the soil in the nesting chamber after it has reached its desired dimensions. One pair abandoned its nest for 22 weeks before use.

Most burrows (86%) are enlarged at a steady rate for two months (Fig. 7.5); however, on many occasions, knowing that todies were actively digging, I sat nearby for hours and never saw the owners. This seems in part due to their irregular regime but perhaps also to their wariness. Skutch (1945b, 1947, 1954) observed motmots to be shy and very difficult to watch at all stages of the nesting cycle, whereas I found todies to be cautious only during excavation.

During the early phases of tunneling, trips to the hole during a digging bout are numerous, and accompanied by rapid, even frenzied, activity (up to 60 visits/hr). These irregular bursts of hyperactivity later settle into an indefinite morning routine, with some pairs visiting the nests to dig for 10 to 15 min, having returned after 30 to 45 min of foraging. Cloudy or rainy days and afternoons suppress building activity. In contrast to the morning work of todies, at least one motmot (Turquoise-browed) prefers afternoon activity (Skutch, 1947).

The hole diameter is established by the time the burrow is 5 to 6 cm

deep (data from 10 nests). As the hole lengthens, more time is spent digging. When the burrow is from 0 to 18 cm long less than 1 min is spent during a visit, but when the hole is 18 to 24 cm deep 1 or 2 min are spent, and later when it is 24 cm or longer the bird stays inside for 2 to 3 min. When enlarging the chamber a bird may remain within the excavation up to 15 min and the frequency of the trips to the burrow decreases.

Multiplicity of Burrows

Many burrows are abandoned before completion. Because both the weather and soil are more variable in the rainforest than in the xeric scrub, one

TABLE 7.2

NUMBERS OF BURROWS ATTEMPTED AND USED IN TWO HABITATS IN PUERTO RICO [1)]

	1968 - 1969		1969 - 1970		Ratio of nests begun to nests used for both seasons combined
	Attempts	Used	Attempts	Used	
RAINFOREST	97	30 (31%)	165	58 (35%)	3 : 1
XERIC SCRUBLAND	38	20 (53%)	16	13 (81%)	1.6 : 1
BOTH HABITATS	135	50	181	71	2.6 : 1

1) No. nests = 316

TABLE 7.3

REASONS FOR ABANDONED BURROWS IN *Todus mexicanus* [1)]

BUILDING STAGE	
1. Unsuitable soil (too sandy, rocky, brittle, clayey, hard, limey, sticky; insufficient or overabundance of plant stabilizer)	30%
2. Bank slippage from heavy rain	12%
3. Bad building techniques (ran into bottom of overhang, begun at too sharp or too steep and angle)	
4. Rapidly - growing ferns or roots obscuring hole	2%
5. Miscellaneous Reasons	53%
a) Occupation by lizard, frog, scorpion, whipscorpion, tarantula, cave cricket	
b) Slightly better spot chosen in same bank	
c) Too early in season	
d) Unknown reasons	
INCUBATION STAGE	
1. Wet nests due to excessive rain	
2. Waterfall in front of nest	2.7%
3. Human interference	
4. Unknown small predators	
NESTLING STAGE	
Chicks starved to death due to weather	0.3%

1) Data from 261 burrows in Luquillo rainforest, Puerto Rico

would expect that more attempts would be required to construct a burrow in the former locality; and this is what has been found (Table 7.2). Rainforest todies begin three times as many burrows as they will ultimately use for egg laying, while scrubland birds start only about 1.6 times as many. In other words, in the former habitat they spend approximately twice as much of their time-energy budget in burrow building.

Ninety-eight per cent of the tunnels are abandoned during excavation, although as the breeding season advances the liklihood increases sharply that once a burrow is begun it will be completed and used (Fig. 7.4). Unsuitable soil and bank slippage from heavy rain are the primary reasons for failures (Table 7.3).

Nest abandonment is not unique to Puerto Rican Todies; although I visited Jamaica and Dominican Republic during the breeding season, over three-quarters of the holes I studied were old, unfinished, and less than 18 cm long.

Some hole-nesters (e.g., Kingfishers) may abandon partly dug holes, or dig short additional holes for sleeping and protection from unfavorable weather (Bent, 1940; Cornwell, 1963; Moreau, 1944, Skutch, 1957; Pettingill, 1970). Two species of motmots in Central America prepare their new burrows immediately after the breeding season, when the soils are soft and pliable from frequent rains. The Blue-crowned Motmot (*Momotus momota*) then leaves it unoccupied for several months until the dry breeding season, while the Blue-throated Green Motmot (*Aspatha gularis*), living at cold, high elevations, uses it as a sleeping dormitory until the following March (Skutch, 1945b, 1964). These motmots have the added advantage of nesting in old-looking holes, less likely to be noticed by predators. As their holes are much longer than those of todies (up to 200 cm), motmots may have to be more careful than todies in the selection of nest sites. In spite of the habits of other Coraciiforms and Rolle's (1960) assumption regarding *Todus mexicanus*, I do not think that todies utilize old burrows for protection from stormy weather.

Proximity to Earlier Burrows

As is to be expected in a species retaining year-round pairs and territories, *T. mexicanus* generally builds near earlier burrows. Of 561 attempts, 89% were within 10 m of an existing burrow. However, in the rainforest where there is an abundance of suitable banks, only 10% of the 1970 burrows were less than 9 m from those constructed by the same pairs in 1969. On the other hand, in Guánica scrub, where banks are much scarcer, 28% of the second season's burrows were less than 9 m from those of a year earlier.

Each year todies excavate anew, although some old sites are renovated for reoccupancy. Roughly 10% (21) of burrows begun in the rainforest in 1970 were improvements on previous holes, and of those 14% (3) were successfully completed.

BURROWS

One fresh burrow of *T. angustirostris* located in a humid gully at an altitude of 1800 m showed obvious indications of having been used previously.

Other Occupants of Burrows

During the examination of over 500 fresh and old tody burrows, I found a variety of nonavian occupants. I can, unfortunately, only speculate on their effect upon the todies. Without obvious enlargement of their entrances, five nests lost 12 eggs. Presumably one or more of the animals considered below was responsible.

Treefrogs

I found *Eleutherodactylus portoricensis* (44 mm long) and *E. richmondi* (32 mm) in six full-sized tody burrows. Drewry (pers. comm.) has also found *E. hedricki* (35 mm) as a burrow occupant. Daylight retreats for the nine species of treefrogs which are abundant in the Puerto Rican rainforest include tree cavities and holes under rocks and in banks. As treefrogs are strictly territorial, they may remain for a considerable period after occupying a fresh tody hole. One large *E. portoricensis* moved into a newly constructed burrow less than one month after its completion and dwelt there for at least 10 months, while at another hole a frog moved in immediately after the nestlings had fledged. In a dry riverbed adjacent to scrub in the Dominican Republic's Cordillera Central, I found a small frog (probably *Eleutherodactylus*) occupying an old burrow made by *T. subulatus*.

Anoles

The small *Anolis* lizards, chiefly four species which grow to 190 mm long, are ubiquitous and abundant in all habitats. I found *A. gundlachi* living in five completed tody burrows, while *A. cristatellus* and *A. evermanni* often crawled in and out of holes. Two anoles moved into a tody nest during construction, one living in the subsequently abandoned hole for several months. Attewell (1907) found a Jamaican anole in a burrow constructed by *T. todus*.

Scorpions (*Tityrus Obtusus*)

I found one of these small stinging arthropods (80 mm) in a burrow at Guánica two days after the three young had fledged. Attewell (1907) reported scorpions in the holes of *T. todus*.

Stinging Ants

Small, red, fiery-stinging ants (*Solenopsis geminata*) occasionally interfere with nesting todies. Once a swarm had completely filled a tody burrow a few days after the young had fledged. I checked the nest two days before the expected fledging of the three chicks; three days later the tunnel was teeming with ants, the entrance was barely visible, and no young todies

were nearby. At another nest ants invaded the day that a nestling fledged. The fledgling survived only one day. It is probable that ants were attracted to excreta and/or decaying birds in the nests, forcing the nestlings to fledge prematurely, whereupon they died.

In Puerto Rico these ants prefer sunny places, especially in sandy or loamy soil, and are much less frequent in shady woods and damp locations. As well as being highly carnivorous and inflicting severe stings, they carry harmful bacteria on their feet for at least 24 hours after feeding off infected materials (Wolcott, 1948). Although I have no evidence, it is remotely possible that these ants may infect nestling todies, weaken or kill them, and then invade their burrows.

Snakes

Snakes are rare in high mountains but may be a slight problem to todies in lower montane forest and lowland scrub. One instance of *Dromicus* (? *stahli*) causing abandonment of a burrow containing nestlings was reported by McCandless (pers. comm.). In Central America Skutch (pers. comm.) has no positive evidence of snakes pillaging motmot burrows, but has suspected their activities on several occasions when eggs disappeared with no enlargement of the tunnel entrance. In general, snakes appear to be a minor problem to Puerto Rican birds, in contrast to their predatory importance on the mainland.

Whipscorpions

These nocturnal predators (*Phrynus palmata*) are quite common in lower montane forests, actively seeking dark caves and tunnels, including old tody burrows. They may eat tody eggs. Their enormous, strong-spined pedipalps are extremely powerful, normally being used to grasp and squash spiders and insects; I suspect they could crush thin-shelled tody eggs with ease.

Snake-like Lizards

Although seldom seen, the nocturnal, weak-limbed "Four-legged Snake" (*Celestus pleei;* up to 20 cm long) and legless "Blind Snake" (*Amphisbaena caeca;* up to 25 cm long) are not rare and could conceivably eat tody eggs and young (Drewry, pers. comm.).

Miscellaneous Occupants

Cave crickets (*Amphicausta caribbea*) are commonly found in tody holes, especially in arid areas, occupying them as quickly as two weeks after they are abandoned by the birds.

Spiders, large and small, with or without webs, are frequent tenants of old tunnels, and various moths and other insects also use them as temporary quarters. Probably none of these invertebrates disturb tody activities, except perhaps the large hairy Puerto Rican "Tarantula" (*Cyrtopholis portoricae*),

which, although generally building its own hole, is found occasionally in tody burrows at lower montane locations.

A widespread and common Jamaican land snail undergoes periods of aestivation, hiding in many types of crevices and holes. I found two in old *T. todus* burrows in high elevation rainforest, one reposing about 20 cm from the entrance.

8
COURTSHIP

Among the Coraciiformes, the bee-eaters, cuckoo-rollers, hoopoes, and rollers have striking courtship displays, mostly consisting of aerial flights and tumbles (Bent, 1940; Forbes–Watson, 1967; Fry, 1969; Moreau, 1937; Skutch, 1945b, 1947, 1964; Thomson, 1964). However, courtship appears to be poorly developed in the Alcedines. I can find descriptions of precopulatory activities for only four species. Motmots (*Motmotus momota, Eumomota superciliosa, Electron platyrhynchum*) at times carry leaves or other inedible objects in their bills and communicate vocally with their mates (Skutch, 1964, 1971) and Belted Kingfishers (*Megaceryle alcyon*) sometimes tumble around in small groups, rattling harshly, and "possibly courting" (Bent, 1940).

Todies, lacking complex vocal repertoires, substitute loud mechanical Wing-rattling for vocalizations in both courtship and territorial aggression (Chaps. 3 and 5). As many elements are common to both behavioral categories, it is sometimes difficult to distinguish between the two, especially during their early phases. I have omitted from consideration any observations which could not be categorized unequivocally.

The following account is concerned with *T. mexicanus* unless otherwise indicated, and is based on 37 observations of courtship, mostly of known pairs.

Courtship appears to take place only within the breeding territory; known pairs (78% of total) always limited their activities to within 5 m of the nest site.

During the breeding season todies remain nearer the ground than at other times, with the result that courtship occurred below 3 m, regardless of the height of the canopy, in 80% of my observations.

Todies remain paired all year but, obviously, courtship activities are concentrated in the months of most active nest building and egg laying, February to May (Fig. 8.1).

Displays in *T. mexicanus*

Courtship displays appear to involve five interacting components, which are discussed below and summarized in Figure 8.2.

Chasing

Short chases (from 1 to 1-1/2 m), with members of the pair following each other closely and Wing-rattling are basic. Each Chasing bout has an average of six Wing-rattles, in all lasting less than 1 min. Either sex may initiate Chasing. They pursue each other over straight stretches, in arcs or circles, or dart and weave among low foliage, covering a distance of

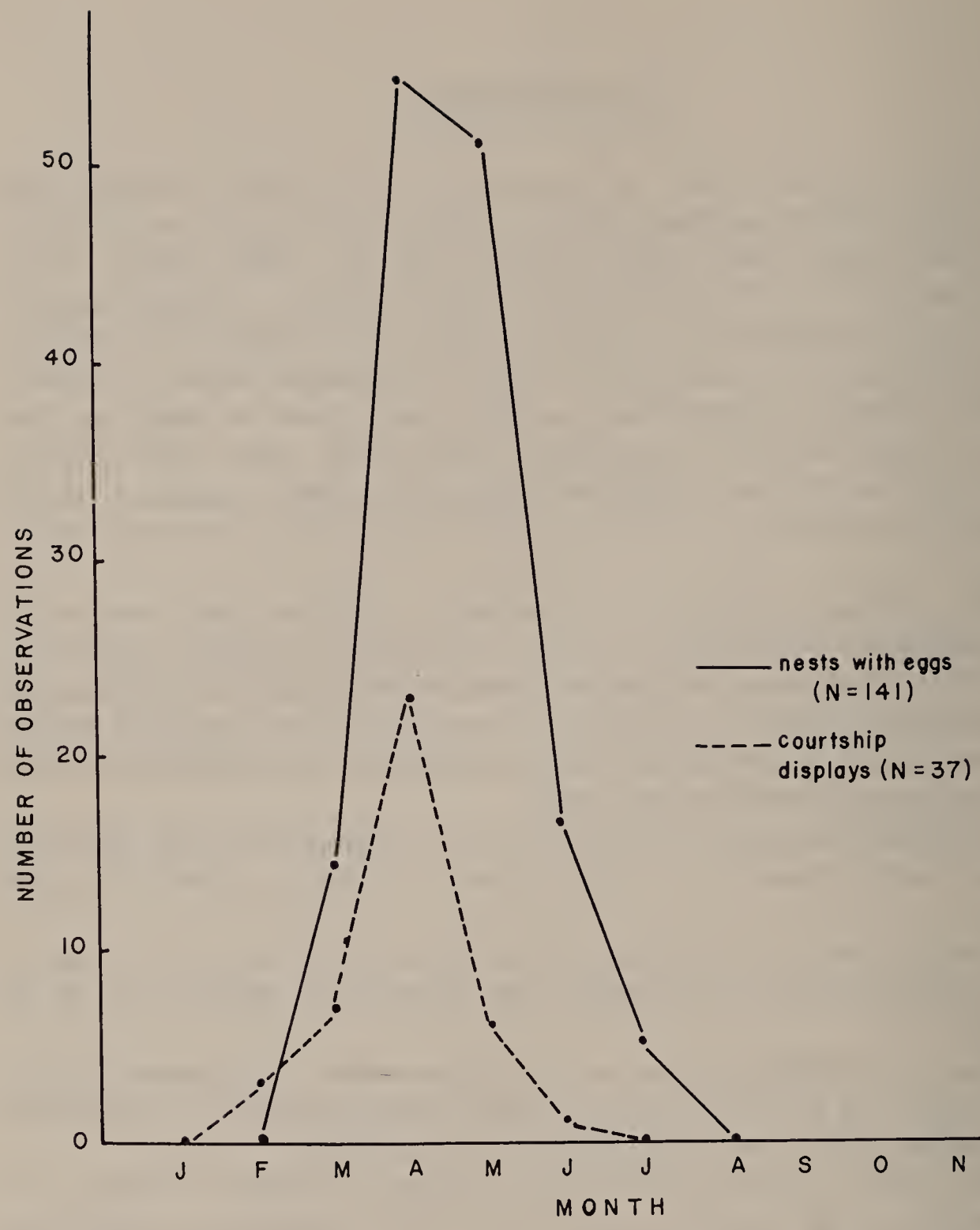


FIG. 8.1 Timing of courtship and egg laying in *T. mexicanus*.

up to 10 m. Most of the close, rapid, Wing-rattling Chases result in body contact. Todies fly vigorously at each other, but less forcefully than in territorial combat.

During the entire nest excavation period the pairbond seems very strong. Hence, after Chasing bouts, todies often perch close to one another, sometimes touching and rarely separated by more than 3–4 m.

WING-FLICKING AND SUBMISSIVE POSTURING

After alighting following Chasing, a female may periodically Wing-flick (Chap. 4), then move to a horizontal position whereupon she slowly flicks

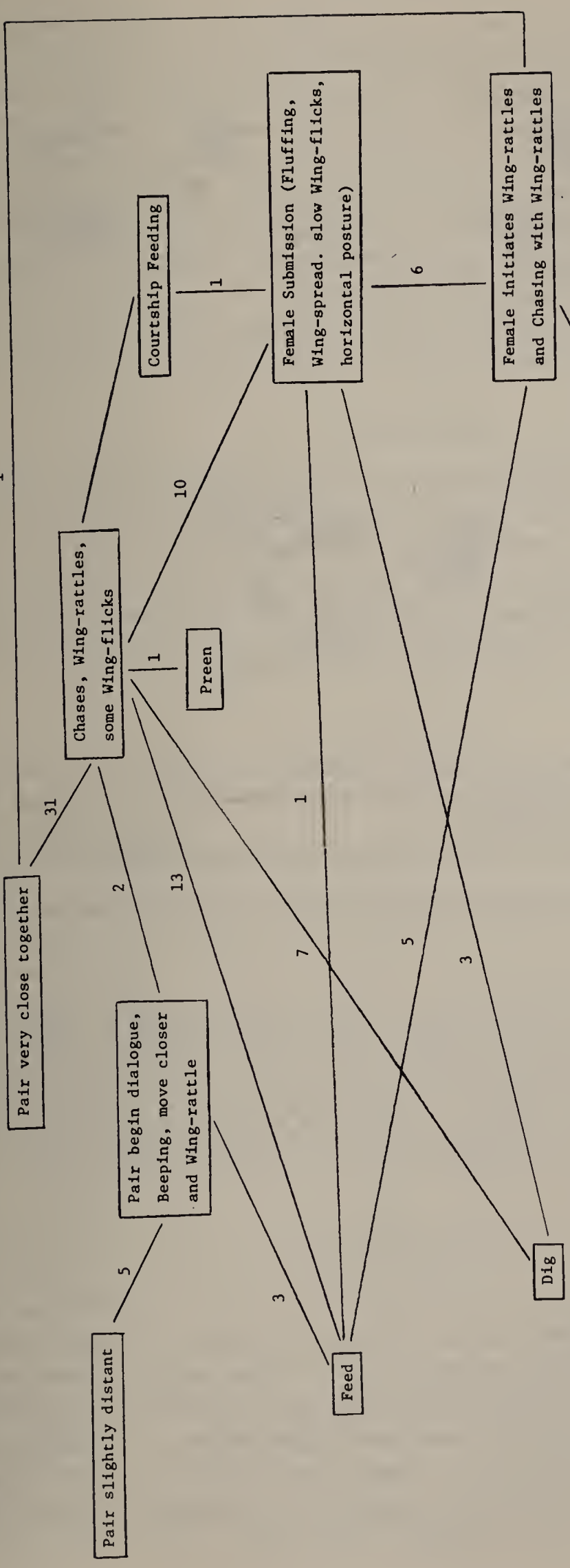


FIG. 8.2 Flow diagram of courtship pattern in *T. mexicanus*. Numerals indicate frequency of observation of given sequence.

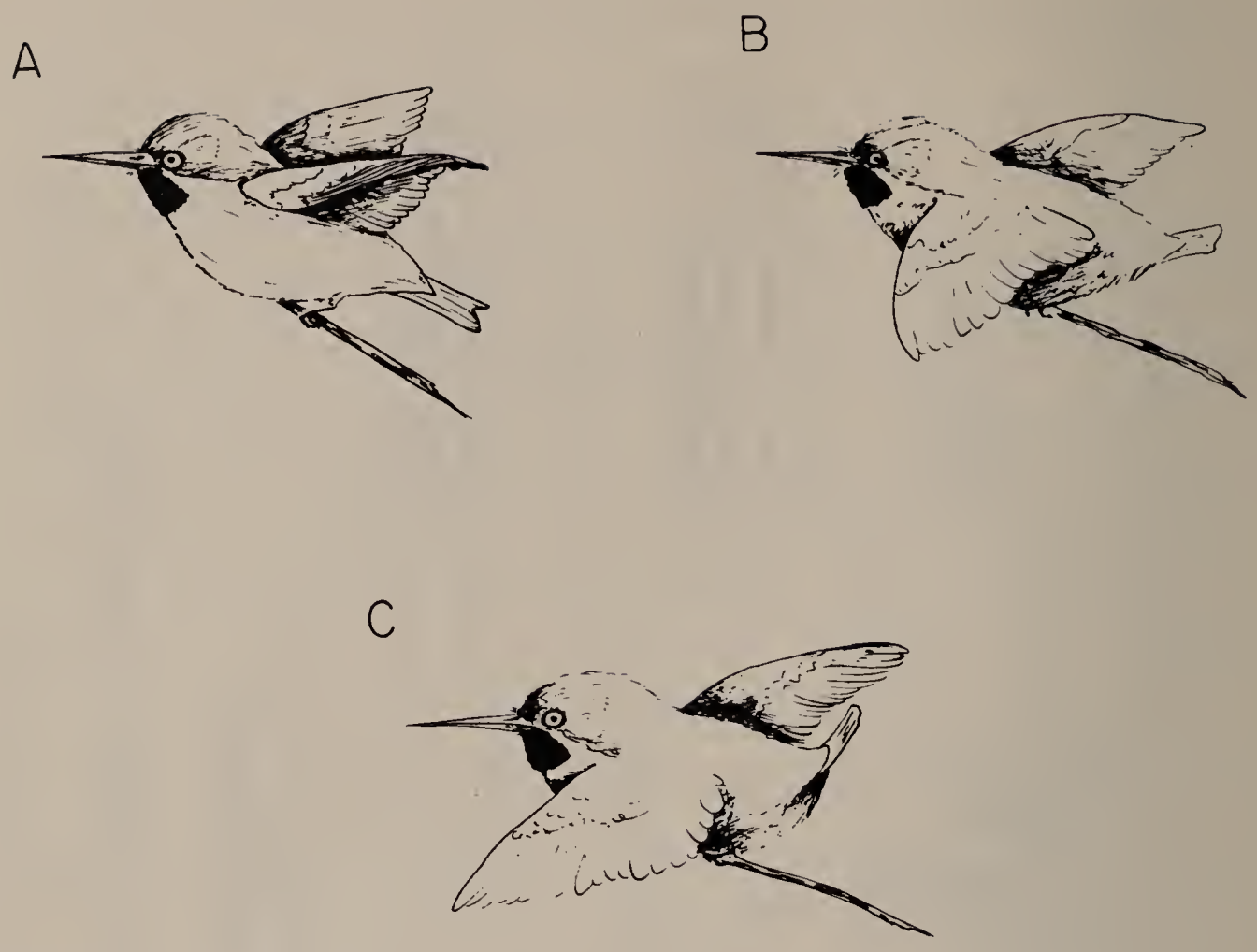


FIG. 8.3 Submissive postures of female *T. mexicanus.*
A. Slow Wing-flick; body partly horizontal, wings flicked slowly, extending wings about one-quarter of full spread.
B. Partial Submission; body horizontal and ruffled, wings about two-thirds spread, tail partly raised.
C. Full Submission; body as in B., but wings fully spread and tail elevated higher.

her wings out farther, pulls the wrists back, and opens her wings about one-quarter of their full extant. Further motivation leads to a horizontal, ruffled posture with the breast touching the perch and the wings approximately two-thirds spread. Finally, in complete submission, she fluffs even more (especially her belly), elevates her tail, and fully spreads her wings (Fig. 8.3).

COURTSHIP FEEDING

Feeding was seen in 6 pairs of *T. mexicanus,* two of *T. todus,* and one of *T. angustirostris.* All three species behaved similarly. In each instance there were no preliminaries, except for a few Wing-rattles in one pair of *T. mexicanus.* One partner flew toward the other, landed or hovered for a moment while exchanging a dead insect (Lepidoptera or Orthoptera), and immediately flew off. Both male and female then resumed foraging, with *T. mexicanus* "males" returning up to three successive times with food items.

COURTSHIP

Courtship feeding in *T. mexicanus* occurred twice before egg laying, three times during incubation and nestling care (when food was given to nestlings), and once after a brood was eaten by a mongoose.

This behavior has been reported from four Coraciiform families, viz., Alcedinidae, Bucerotidae, Momotidae, and Upupidae (Lack, 1940, 1941; Moreau, 1937; Skutch, 1947, 1957). Turquoise-browed motmots (*Eumomota superciliosa*) and Amazon Kingfishers (*Chloroceryle amazona*) courtship feed only during incubation while the European Kingfisher (*Alcedo atthis*) does so during any stage of the reproductive cycle. The male of the Black-chinned Jacamar (*Galbula melanogenia*), another hole digger, regularly supplies his mate with arthropods as she excavates the tunnel (Skutch, 1937).

Vocalizations

While courting, todies always appear agitated, hopping and Bobbing rapidly within the vegetation, fluffing frequently, and seldom feeding or vocalizing. They are silent within the vicinity of the nest, except for low Muttering sounds. Low Beeping, Bee-beeping, and Beeping (sometimes accelerated), Beep-trilling, and Loud Beeping (Chap. 3) may all accompany Chases, but are not predictable nor conspicuous components of courtship.

Copulation

I observed copulation only twice, once in *T. mexicanus* and once in *T. todus*, on sunny days in March and April, respectively, and both between 08:00 and 09:00.

The *T. mexicanus* pair was located 1 to 3 m high in a small bush at the edge of a precipitous escarpment in the rainforest. The male Wing-rattled and pursued the female, touching her body 10 times (1/sec) and each time attempting to copulate but only succeeding once. Then, in complete submission, she flattened her body onto a branchlet, ruffled her feathers, and assumed a horizontal position, allowing the male to mount her, flutter his wings, and grasp her crown or nape feathers for balance. Then following six more chases, all less than a distance of 0.2 m, the male Loud Beeped rapidly and mounted her again. They continued sitting together, Beeping and following each other's movements closely when they darted around in low foliage. Twelve minutes after copulation they began feeding. H. Snyder (pers. comm.) also saw todies copulating in Luquillo rainforest, in late October. The act was accompanied by much Chasing, Wing-rattling, and vocalizations.

As I watched a silent pair of *T. todus* in second-growth Acacia scrub, the male chased his mate for 6 m and as soon as she landed swooped directly onto her rump. Flattening her, he grasped her forehead and crown and proceeded with 29 cloacal contacts, completing copulation in 35 sec. Even though I had located this pair 4 min earlier, and had been in the general area for 20 min, I was unaware of any precopulatory behavior, such as Chases, Wing-rattles, Flank Displays, etc. . . . Less than 1 min after

their separation I heard two Throat-rattles and some Loud Beeps; the birds then Chased before disappearing in different directions.

Additional Displays in other Species

The brief time spent with other species of *Todus* did not enable me to study known pairs for long periods, hence the following information is fragmentary.

Flank Displays

In addition to their territorial function (see Chapter 5), it is possible that Flank Displays play some role in courting activities. Of the 20 Flank Displays seen in *T. angustirostris*, *T. subulatus*, and *T. todus*, several pairs of birds displayed for as long as 2 hr, indicating precopulatory behavior rather than aggression.

Hopping Display

I saw this unusual display only once. It was performed by one member of a pair of *T. angustirostris* which was feeding low in a rainforest high in the Dominican Republic's Cordillera Central. Following 2 hrs of observation, one tody (white iris; sex?) excitedly made six hops along a bare inclined branch, covering a distance of about 30 cm. After each hop the tody spread its wings approximately one-quarter open, remaining there for 1 sec before proceeding. After hopping to the left it returned in the same manner in the opposite direction, finishing at the starting point. It then repeated the whole procedure, hopping the distance four times. The bird stood upright with its breast and flanks puffed out, exposing much pink, and with its bill pointed upward.

The relatively slow Wing-flicking was reminiscent of submission in *T. mexicanus*, except that the tody's body was upright. I saw no other unusual behavior, and after this performance the tody flew off with its mate, Wing-rattled a few times, and disappeared.

Discussion

Courtship in todies shows affinities with other Coraciiforms in having aerial flights and tumbles, and lacking distinctive vocalizations. Wing-rattling gives it a unique touch, and in this respect tody courtship resembles that of the Passeriform manakins (Pipridae), whose wing-cracking lek displays are much more elaborate (Sick, 1967).

As in many vertebrates, courtship and aggression are closely interrelated. It will only be through further study of banded pairs of all species that the description of precopulatory behavior in the Todidae will be completed and its evolution postulated. It is possible that Flank Displays, which are virtually absent in *T. mexicanus*, play a major role in the courtship of other species, perhaps contributing to the various isolating mechanisms that separate the two Hispaniolan species.

9
EGGS AND INCUBATION

Eggs

The eggshell is immaculately white when the contents are removed, but in life it has a warm rosy tinge due to the large orange-red yolk. The shells are glossy and extremely fragile.

Measurements

Tody eggs are the smallest within the Coraciiformes. They are roughly the size of those of small wrens (*Troglodytes* spp.) and larger than those

TABLE 9.1

EGG MEASUREMENTS

	NO. EGGS	LENGTH (mm)	WIDTH (mm)	WEIGHT	REFERENCE
angustirostris	5	15.1 - 15.7 (15.5)	13.0 - 13.7 (13.5)	-	Wetmore & Swales (1931); Bond (1949)
mexicanus	17	15.6 - 17.5 (16.0)	13.0 - 14.3 (13.5)	1.38 - 1.46 (1.44)	Rolle (ms); Wetmore (1916) USMN specimens;this study
multicolor	6	14.6 - 16.0 (15.5)	11.8 - 13.4 (12.6)	-	C.T.R., USMN specimens
subulatus	39	15.9 - 18.8 (16.9)	13.3 - 15.1 (14.3)	-	Ciferri (USNM); Cory(1885) Wetmore & Swales (1931); Bond (1949)
todus	28	14.9 - 17.0 (16.1)	12.8 - 14.0 (13.3)	-	March & Maxon(USNM)

of most hummingbirds. Table 9.1 lists the egg measurements from the five species of *Todus*. Their eggs are ovate. Those of *T. multicolor* are the smallest, while those of *T. subulatus* are the largest. Bond (1949) found that the eggs of *T. subulatus* from Gonave Island were smaller than those collected on the mainland, even though the birds themselves are slightly larger on Gonave.

Five eggs of *T. mexicanus* weighed an average of 1.44 g, which represents 26% of the bird's body weight. It is generally recognized that small birds lay relatively heavier eggs than large birds. In most birds egg-to-body weight ratios vary from 11% down to 1.8% (Thomson, 1964). Some birds with long incubation periods, such as kiwis (*Apteryx*, 75–77 days) and small petrels (*Hydrobates*, about 40 days), are renowned for producing eggs which are 20 to 25% of their body weight. The tody's 26% is very high and is higher than those of similar-sized hummingbirds, which appear to run about 11 to 15%. The relative heaviness of tody eggs is due to the large yolk reserve required for the long incubation period (21 to 22 days). The small, highly

active, insectivorous Tody-flycatchers and Tody-tyrants also have relatively high egg-to-body weight ratios (18% for *T. maculatum;* Haverschmidt, 1968), which undoubtedly is related to their similarly long incubation period (19 days).

Clutch Size

Three to four weeks usually elapse between the completion of the nest and the laying of the one to four glossy eggs in the bare, unlined chamber.

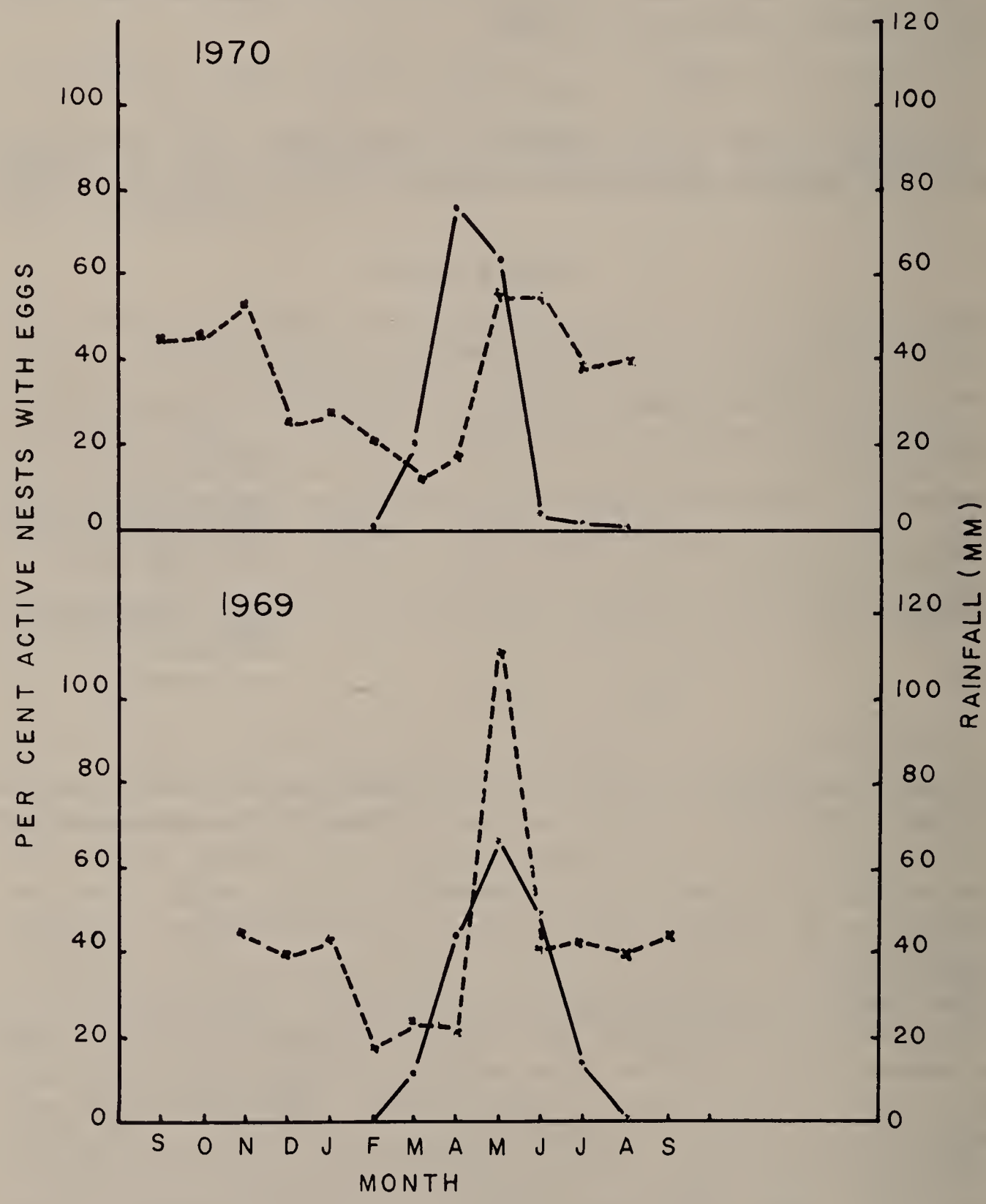


Fig. 9.1 Influence of rainfall (dashed lines) on peak egg laying (solid lines) in *T. mexicanus.* Data are from 85 nests in Luquillo Forest during 1968–1969 and 1969–1970. Note how the drought accelerated egg laying during spring 1970.

EGGS AND INCUBATION

Rolle (1960) reported a clutch size of two to six, but I find no reference to such a large clutch in his personal notes or elsewhere. There is, however, in the USNM egg collection, a 1919 note by Abbott that clutches of *T. angustirostris* are "usually four to five eggs." Considering their extremely high metabolic rates, I doubt that todies could raise six young.

The mean clutch size for *T. mexicanus* in the Luquillo rainforest was 2.39 (N = 44) and in the Guánica xeric scrub 2.22 (N = 9), giving a combined average of 2.36. Four *T. todus* clutches averaged 2.8 eggs (Attewell, 1907).

Clutches were significantly larger ($.050 > p > .025$) in nests with helpers (av 2.9) than in nests where only two adults attended the young (av 2.3). Other effects of nest helpers will be discussed at the end of this chapter and in Chapter 12.

Incubation

Timing of Egg Laying

Throughout Puerto Rico eggs are laid between March and July, with the peak laying time differing according to habitat and weather conditions. I found the earliest eggs at Luquillo during the last week of March.

In the rainforest todies normally build and lay eggs during the driest part of the year. An unusually long, island-wide, dry season occurred during the spring of 1970, which accelerated digging, courtship, and egg laying by three to four weeks at Luquillo. In xeric scrub, where rainfall is one-seventh of that in the rainforest, todies build, incubate, and rear their young as far as possible into the "wet" season. Generally there is a two week difference in peak breeding activities between the rainforest and dry scrub, but the 1970 drought turned this delay into six weeks (Figs. 9.1 and 13.3).

Todies lay eggs on consecutive nights until the clutch is complete. They do not attend the eggs during the day while laying is in progress, but presumably incubate at night, as the nestlings hatch asynchronously.

Usually one clutch is laid each season, although three pairs of birds in the rainforest attempted multiple nestings after their eggs or young were lost. A single brood annually is characteristic of other Coraciiforms, although there are exceptions such as the Half-collared Kingfisher (*Alcedo semitorquata*) which is typically double-brooded (Moreau, 1944).

Incubation Period

Owing to the difficulty of observing the bird in its chamber, and to the bird's habit of not attending completed nests for about two months before laying, data on the incubation period (time between laying of last egg and hatching of final chick) was obtained from only one nest. Here the incubation period was determined to be 21 to 22 days at a nest attended by two adults.

This period is longer by several days than that of any comparable-sized hole- or cup-nester (Table 10.1), and is close to that of the Slaty-headed Tody–Tyrant (*Todirostrum sylvia*), a pensile nester with a particularly long

incubation period (19 days). The 15 species of *Todirostrum* also have high metabolic rates similar to those of todies (see Chap. 6); their convergence in egg-to-body weight ratios has been mentioned earlier in this chapter. Pensile nesters usually have incubation periods longer than cup-nesters and shorter than hole-nesters (Skutch, 1945a).

Possible reasons for the tody's long incubation period are discussed below.

Incubation Behavior

Rhythm of attentiveness.—Both sexes develop brood patches and both incubate, although the female assumes the larger share of the task. They are, however, by no means predictable in attentiveness. Their visits ranged from 27/sec to 58 min; the average time per visit rises from an initial 2 min to a maximum of 16 min, decreasing slightly prior to hatching and continuing to drop through the nestling period (Fig. 10.5). The average time per visit for the whole incubation period is only 13.1 min.

It can be seen that todies are unusually inattentive during incubation. Each nest visit averages only 13.1 min and each adult spends *less than one-quarter* of its time incubating. If helpers are present, the time spent incubating by each adult is even less. Data for three species of motmots and five species of kingfishers indicate that they spend up to seven continuous hours on eggs, keeping them almost constantly covered. Even the Half-collared Kingfisher spends 1–2 hr at a sitting throughout the day. The members of the pair of the Ringed Kingfisher (*Alcedo torquata*) and Blue-crowned Motmot change-over only once a day (Skutch, 1945a, 1957, 1964; Moreau, 1944).

The only explanation I can suggest for such inattentiveness is related to feeding habits. It has long been known to West Indians and zoo personnel that todies are virtually impossible to keep in captivity. After many trials, one was finally kept alive for a short time in the Bronx Zoo, New York City; it was calculated that todies ate at least 40% of their body weight in live insects each day (Griswald, 1959). My research indicates that this is an excellent calculation; field observations show that todies average two insects every minute from dawn to dusk at Guánica, and about one insect/min at Luquillo (Chap. 6). Observations from mistnetting indicate that during the daytime todies can survive little more than an hour without food.

The short, irregular intervals of incubation probably indicate that high metabolism and an insectivorous diet require todies to feed far more frequently than their Coraciiform relatives. The fact that todies have very short intestines (barely 7 cm long), roughly equal to their body length (Clark, 1913), although two intestinal caecae are present (Forbes, 1882), is doubtless a further indication that food passes through the alimentary tract with great rapidity.

Skutch (1945a) found that some small flycatchers (e.g., *Todirostrum*) devote much time to foraging during the nesting season, spending less than 60% of the day incubating, which he considers a "very poor record." This is

another area in which *Todus* and *Todirostrum* converge.

Nest relief.—Coraciiforms do not have the elaborate greeting ceremonies seen in some other hole-nesters (e.g., woodpeckers, jacamars).

In todies the change-over signal is usually one or two sharp Beeps, uttered as the bird arrives in the vicinity of the nest. At times several regular Beeps appear to be sufficiently communicative; these increase in intensity as the nonincubating partner approaches the burrow. Less often an adult flies to the entrance of the hole, hovers for a moment in midair with a faint wing-whirr, then returns to its "favorite perch" or Beeps softly before flying straight into the hole, ousting its mate, as do motmots and kingfishers. Because immediate change-over is rare, parents do not always appear to communicate as they enter and exit after an attentive period. When a bird emerges, it flies off, either alone or in company with its mate, to forage for periods up to 85 min (av 13 min) before returning. Motmots and kingfishers, on the contrary, are quite predictable at change-over (Skutch, 1945b, 1947, 1957, 1964; Bent, 1940).

Inside the burrow.—Incubating birds always orient toward the light. Both sexes develop brood patches.

Outside the burrow.—Todies are very silent around the nest; occasionally I heard a few soft Beeps and sharp Beeps, but they never Wing-rattled when entering or leaving burrows. Their coordination and eyesight enable them to fly, without decelerating, in a direct line from as far as 8 m away, straight into the small entrance barely bigger than their own diameter. They usually enter from one of two or three "favorite perches" but sometimes fly in suddenly from another direction, without giving an audible warning. Sometimes I watched a burrow intently for an hour or more from only 10 m away and still missed the birds as they entered or left.

On leaving the nest they usually fly out to forage beyond the vicinity of the burrow, but if they remain nearby they often feed close to the ground, as they do during nest excavation.

Bill-gaping, Regurgitation, Fluffing, Preening, and silent Bobbing commonly occur while near the nest site.

Nest defense typically involves aggressive postures and Wing-rattling (Chap. 5).

Nest Helpers.—This interesting phenomenon is discussed in Chapter 12. Briefly, in four of 23 closely observed nests (13%), helpers began to assist during incubation.

10
CARE AND DEVELOPMENT OF YOUNG

Hatching

Time

Data from six nests indicate that six chicks (and probably five others) hatched later than 15:00 (70% of total), one before 10:00 (7%) and two others at unknown times. Although there is no direct evidence, todies probably have a relatively large reserve of yolk at hatching, thus allowing them to defer feeding for a lengthy period. If this were not true, one would expect evolutionary pressure to favor hatching early in the day, so that the young could be well-nourished before nightfall.

Information on hatching times of birds nesting in relatively inaccessible places is scarce. Rough-winged Swallows, *Stelgidopteryx ruficollis* (Lunk, 1962), Southern House Wrens, *Troglodytes musculus* (Skutch, 1953), and Blue-crowned Motmots, *Momotus momota* (Skutch, 1945) hatch throughout the day. Nests within holes experience relatively constant darkness and a uniform temperature, and are less vulnerable to predators. It is, therefore, probable that the time of day when hatching occurs is less important to hole-nesters than it is to other birds. Nevertheless, the fact that todies seem to be predominantly late afternoon hatchers suggests that there must be some, as yet unknown, significance to this.

Even though the eggs are laid on consecutive days, a clutch of three usually hatches within only a two-day period, probably because of irregular incubation prior to completion of the clutch.

Process

I watched two nestlings emerge from the eggs, and glimpsed others at various stages. The process does not necessarily result in two equal-sized shell halfs; I often found one large section of shell and many smaller fragments.

Limited observations indicate that hatching, although a continuous process, can be divided into four stages: (1) Exerting pressure with its egg-tooth, the chick pips the egg, forming a small irregular hole roughly in the center. (2) The chick works around the circumference of the egg at right angles to its long axis. (3) It completes this cleavage, either emerging as in other birds from two half-shells, or it begins another break parallel to the long axis of the shell, exiting from one half-shell and several smaller, irregular pieces. (4) The chick, with strong, rhythmic, muscular movements, continually stretches its neck at one end and pushes hard with its abdomen at the other, finally squirming out. It then lies gasping, seemingly totally exhausted, sprawled on its belly on the bare floor of the chamber.

CARE AND DEVELOPMENT OF YOUNG

At no time did I hear sounds from chicks; in fact, squeaking was not heard until the third or fourth day.

Hatching in small birds of similar size varies in time. Twice the young of *T. mexicanus* emerged from newly pipped eggs in less than one hour, while the similar-sized wren (*Troglodytes troglodytes*) normally takes two days (Welty, 1962), and the larger Amazon Kingfisher (*Chlorocerlye amazona*) requires one or two days (Skutch, 1957).

Attendance by Adults

The adult, although present, does not assist the emerging chick. Generally both adults establish a feeding rhythm immediately after hatching.

Disposal of Shell

In common with most Coraciiforms, but in contrast to other hole-nesters such as jacamars and woodpeckers, todies do not remove the shells but allow them to accumulate with excreta on the chamber floor.

Care of the Young

Nestling Period

Data from 12 nests indicate a usual nestling period of 19 to 20 days, with a range from 17 to 22 days, the variation depending on the number of young in the nest, the attentiveness of the parents, and the presence or absence of helpers. For example, a 17-day period was observed when three chicks were fed by four adults, and when one chick was fed by two adults; a period of 19 to 20 days occured when two or three chicks were fed by two to four adults; and a 22 day nestling period was noted when two chicks were fed by two inattentive adults.

The length of the nestling period is similar to that in other small, hole-nesting passerines, both in temperate and tropical regions, even though

TABLE 10.1

COMPARISON OF TODY INCUBATION AND NESTLING PERIODS WITH THOSE OF SOME SMALL PASSERINE HOLE - NESTERS[1)]

		NO. SPECIES	AV. CLUTCH SIZE	AV. INCUBATION PERIOD (days)	AV. NESTLING PERIOD (days)
Todus mexicanus		1	2.3	21 - 22	19 - 20
Passerine hole-nesters					
Temperate	Europe	18	6.9	13.8	17.3
	Asia	10	5.4	13.8	18.8
Tropical	America	8	-	16.0	18.8
	Africa	8	-	14.6	18.8

1) From Nice (1937), Moreau & Moreau (1940) and this study

the clutch size of *T. mexicanus* is smaller and its incubation period is somewhat longer (Table 10.1). Unfortunately, there seem to be no data available for small kingfishers (*Ispidina, Myioceyx*) and for the todies' nearest possible relative, the Tody Motmot (*Hylomanes momotula*); the smallest studied kingfisher (*Alcedo semitorquata;* 16.5 cm) spends 27 days in the nest (Moreau, 1937).

Brooding

Todies brood their chicks for the first few days, which is characteristic of birds with altricial young, although the time spent in the nest is sharply

TABLE 10.2

TIME SPENT IN NESTS BY BOTH ADULTS OF *mexicanus* [1)]

AGE OF YOUNG (days)	PERCENT OF COMBINED DAYLIGHT TIME BUDGET OF PARENTS
0 - 2	50%
3 - 5	24%
6 - 8	2%
9 - 20 +	less than 2%

1) Data represents averages from 29 nests

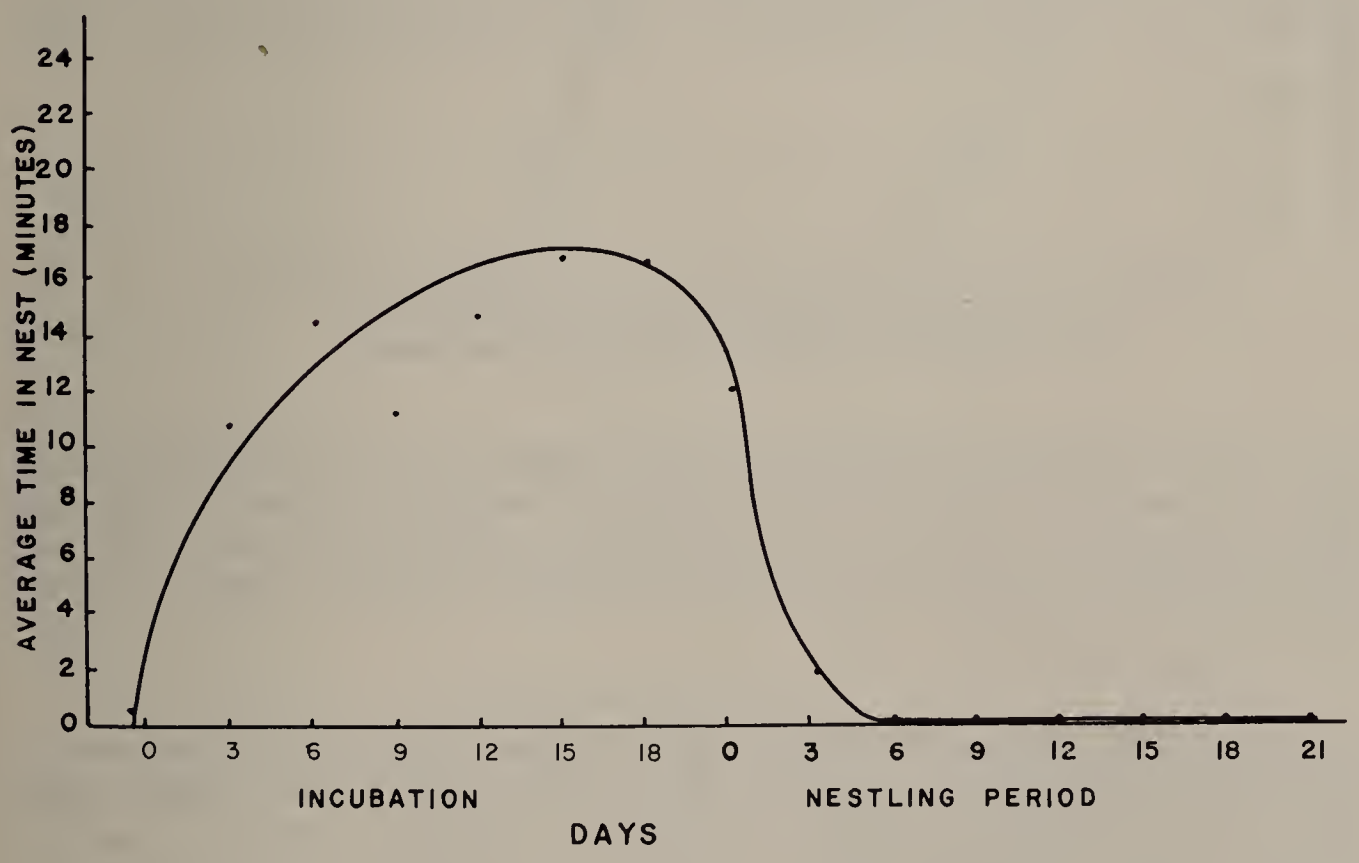


Fig. 10.1 Amount of daylight time spent by adults in nest from egg laying to fledging. Data from 29 nests in Luquillo and Guánica Forests in 1969 and 1970 during all types of weather (151.5 observation hours) and from clutches of one to four eggs. Each point represents an average of a three-day interval, except for the first six days of the nestling period, which are treated individually.

less than that spent prior to hatching (Table 10.2, Fig. 10.1). The young are brooded for the first 37% of nestling period (8 days), which is comparable to the 40% (5 days) of another small, altricial, insectivorous hole-nester, the Carolina Wren, *Thryothorus ludovicianus* (Laskey, 1948). However, cup-nesters are much more attentive; for example, American Redstarts (*Setophaga ruticilla*) spend 90% of the nestling period (6 days) brooding young (Sturm, 1945). The difference between the two groups is doubtless because the young of hole-nesters are less affected by direct sun, wind, and large temperature fluctuations, and therefore can be left unattended sooner, and more often (Fig. 10.2).

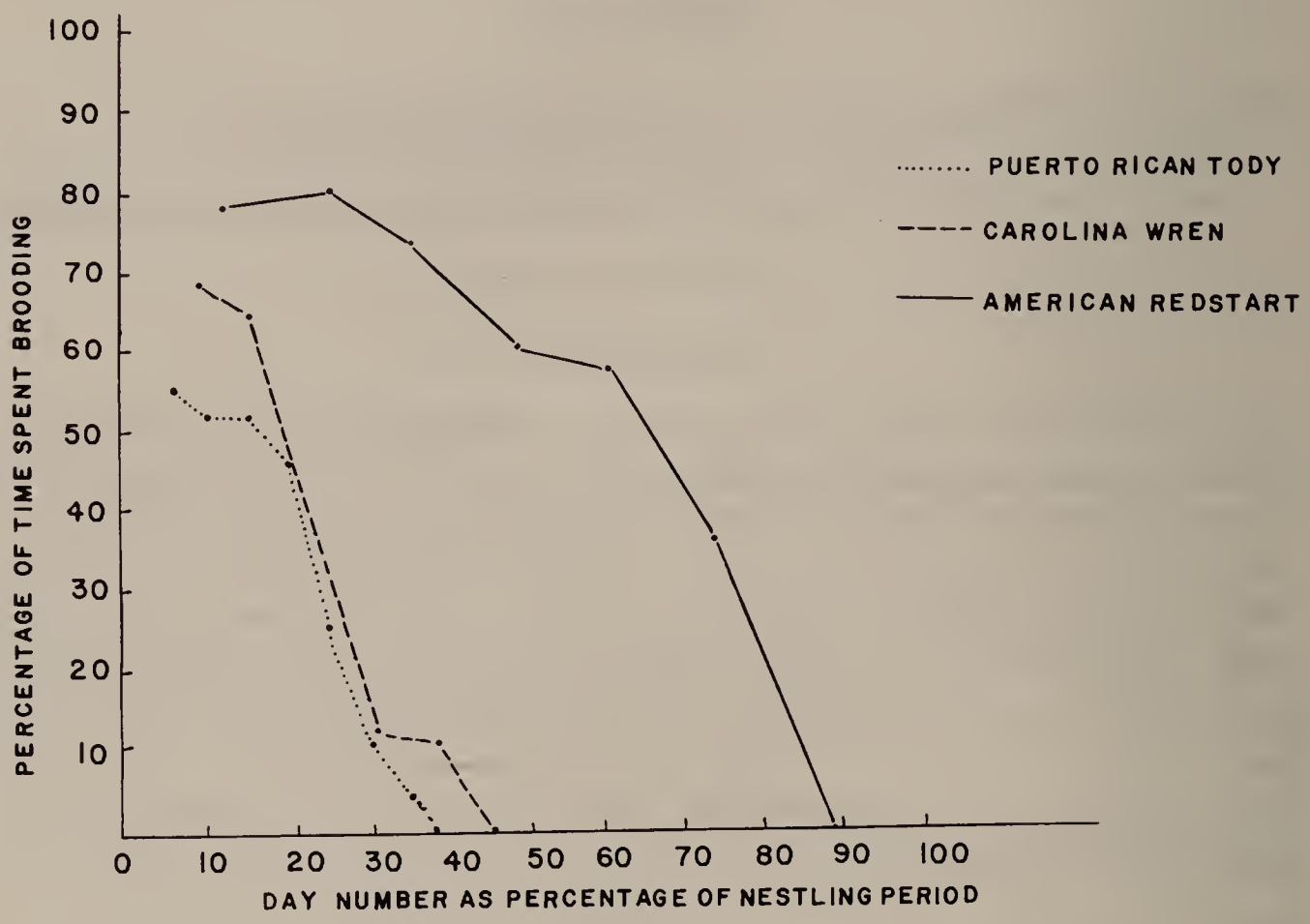


FIG. 10.2 Brooding interval relative to total nestling period in the Puerto Rican Tody (*T. mexicanus*), Carolina Wren (*Thryothorus ludovicianus*), and the American Redstart (*Setophaga ruticilla*). The total time spent brooding is similar for all three species (see text), but for each the brooding period represents a different portion of the total nestling period.

Even though the *number* of days and the *percentage* of the total nestling period spent brooding are similar to those of other small hole-nesters, todies spend much less time covering their chicks (average of 39% of combined daylight hours in seven days). The longest brooding period was 25 min, but the average was only 5.7 min/visit. In the Southern House Wren, for example, nestlings are brooded 90% of the daylight hours until day 10 (total nestling period 18 days), at which time the chicks are well-feathered (Skutch, 1953).

CARE AND DEVELOPMENT OF YOUNG

Feeding

General Adult Behavior

A general pattern and sequence of adult behavior emerges during the 19 days of nestling life: (1) Both sexes participate in feeding chicks, although the male takes the greater share. (2) They feed close to the burrow (up to about 15 m) while Beeping. (3) They return to the vicinity of the nest (4–5 m from the hole), sit on a twig, and often immobilize food. They are generally silent or may utter a few Beeps or low Beeps; Bobbing may occur. (4) After flying to their "favorite perches" they either sit silently or thrash the insect further. Very seldom do they Preen, Fluff, or Regurgitate—behavior commonly seen close to the burrows that are under construction. Generally, two or three todies remain near the nest, especially when attending older chicks. Many times as many as four adults await their turn to enter the burrow with food. (5) As a tody swoops into the hole it utters a soft Beep, which elicits responses from the nestlings, if they are old enough to have begun to squeak. (6) Even though each member of a pair follows the other's movements closely, doubling-up within the chamber and near collisions do occur. (All 10 instances in which adults were in the nest simultaneously occurred during the first few days after hatching, when an adult brooded after feeding the chicks. The overlap was usually less than one minute.) (7) Until the seventh day an adult remains in the nest for a variable period (av 5.7 min); later the visit averages only 6 sec/trip. (8) When leaving the bird peers for a moment from the burrow entrance,

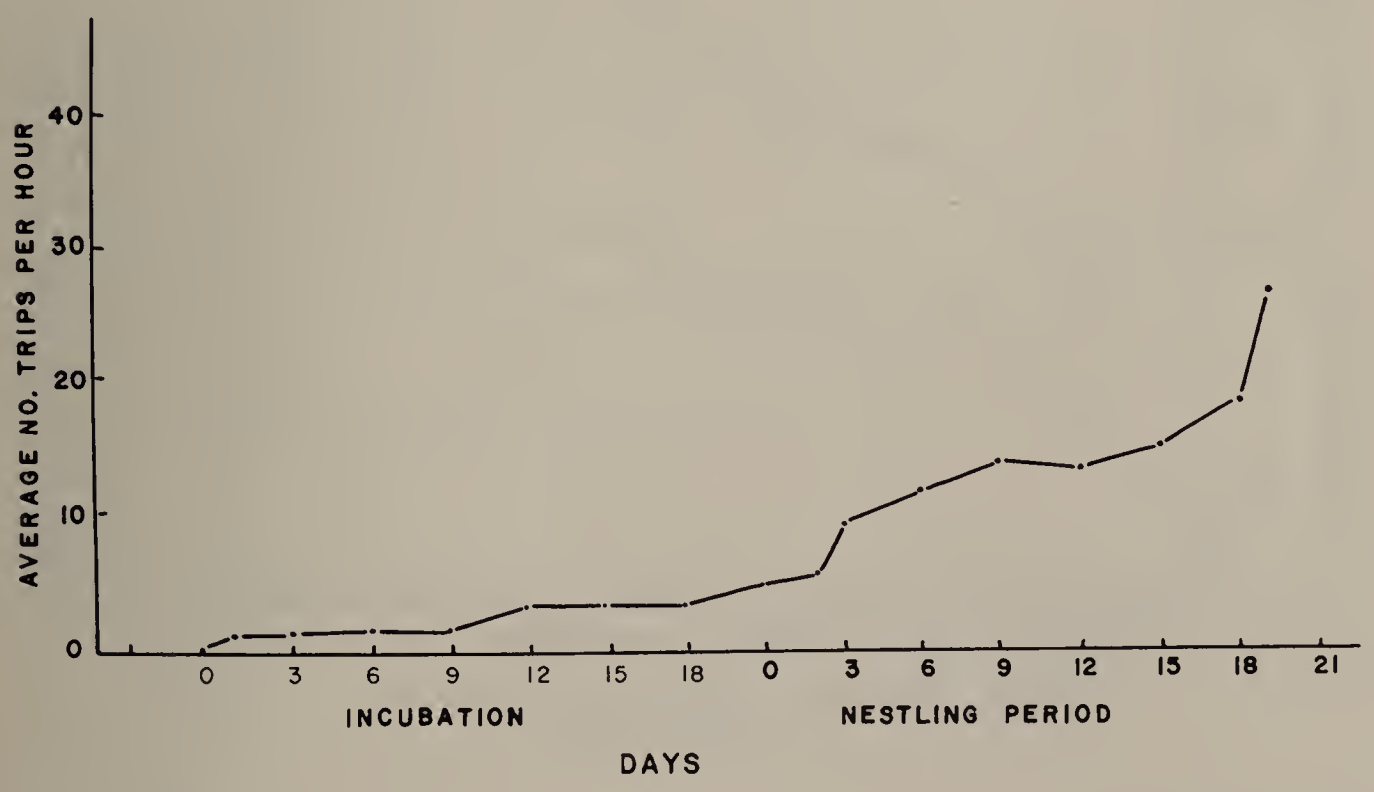


Fig. 10.3 Number of nest visits during incubation and nestling periods. Data from 743 visits at 29 nests in Luquillo and Guánica Forests (151.5 observation hours) taken in 1969 and 1970 during all types of weather and from clutches of one to four eggs (av 2.2). Each point represents an average of a three-day interval.

flies out (usually in a fixed direction opposite to the entering path), and then forages. The tody sometimes snatches an unwary insect on its smooth outward flight, but does not decelerate until it is about to land.

Rates

The number of hourly nest visitations increases steadily from hatching (av 5) to fledging (av 27). The overall number of hourly visits averaged 10.8, equivalent to 4.9 feedings/nestling/hour (Fig. 10.3). Corresponding

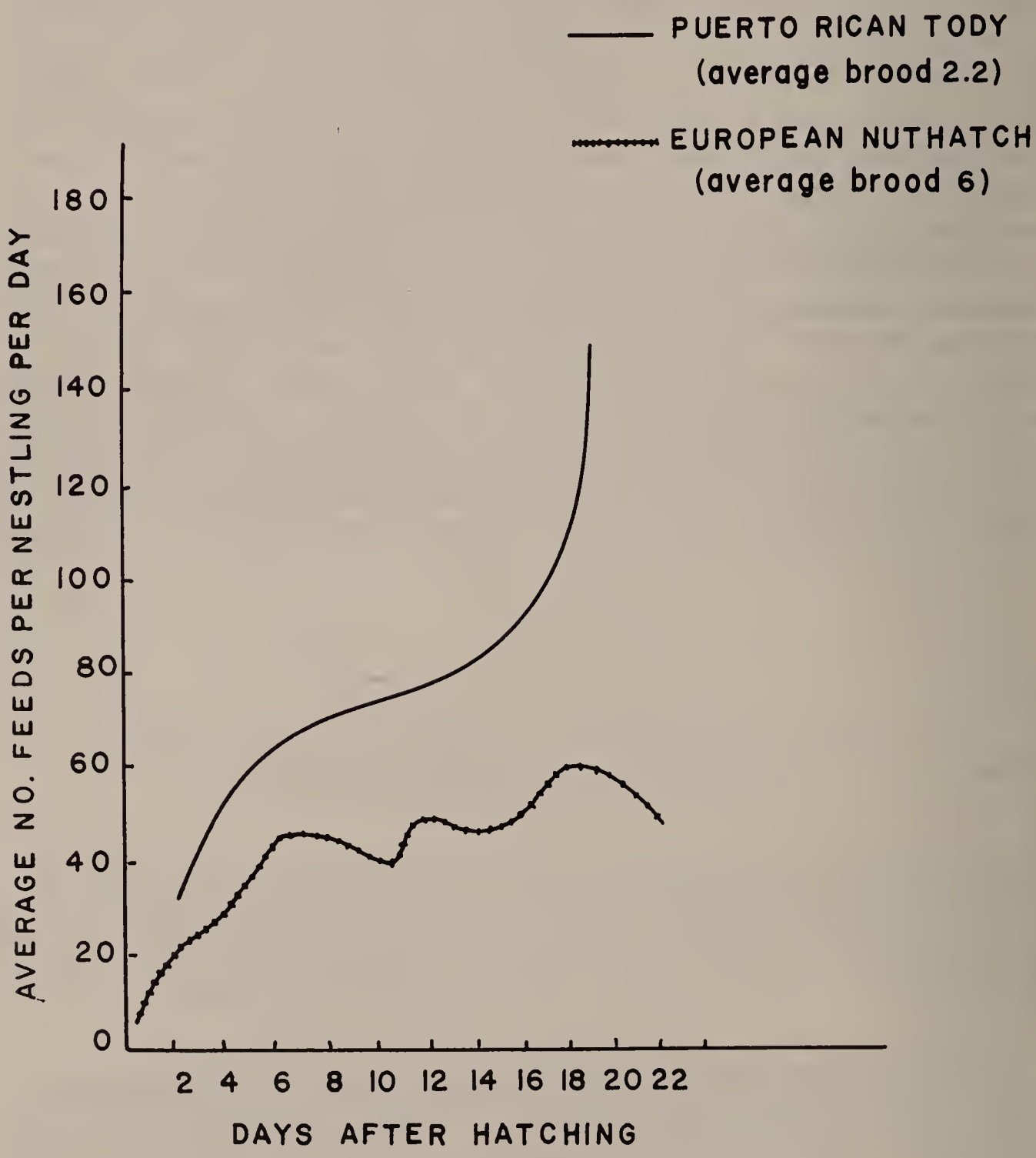


FIG. 10.4 Feeding rates for nestlings of *T. mexicanus* and the European Nuthatch (*Sitta europaea*). Data are from 29 tody nests in Luquillo and Guánica Forests, taken during all types of weather in 1969 and 1970 (94 observation hours), and from Bussman (1943, *in* Welty, 1962: 330). Note the decline in feeding rate prior to fledging in *Sitta europaea*.

figures for the cup-nesting American Redstart and hole-nesting Southern House Wren, are 3.4 and 3.8 (Sturm, 1945; Haverschmidt, 1952). Let us compare *T. mexicanus* with a typical small hole-nester, the European Nuthatch (*Sitta europaea,* 13.8 cm; Fig. 10.4). As well as a *lower feeding rate per nestling,* the nuthatch typifies a *decline in feeding rate* before fledging, a widespread phenomenon possibly reflecting ". . . fatigue of overworked parents, or a naturally-evolved device to encourage the newly-fledged young to leave the nest and seek their own food" (Welty, 1962: 330).

Todies appear to accelerate their nest visitations prior to fledging; the highest rate was on the penultimate day. Four attending adults waited in turn to deliver food to two chicks at a rate of 35 visitations/hr. This continued for 5-1/2 hr (90:00 to 14:30) and later observations indicated that the speed had not slackened. Assuming a 12-hour period of daylight available for gathering food, this high rate of feeding resulted in *140 feedings per chick per day.*

For comparison, the Great Tit (*Parus major*), with feeding rates up to 112 feedings/nestling/day for eight chicks is often quoted as an extreme case in parental feeding (Perrins, 1965). Additional data from warblers, chickadees, nuthatches, and wrens indicate that they all feed their young at a slower rate (and show a decline toward fledging), as well as for a shorter period than do todies. One must conclude that nestling todies, like their parents (Chap. 6), must have extremely high metabolic rates.

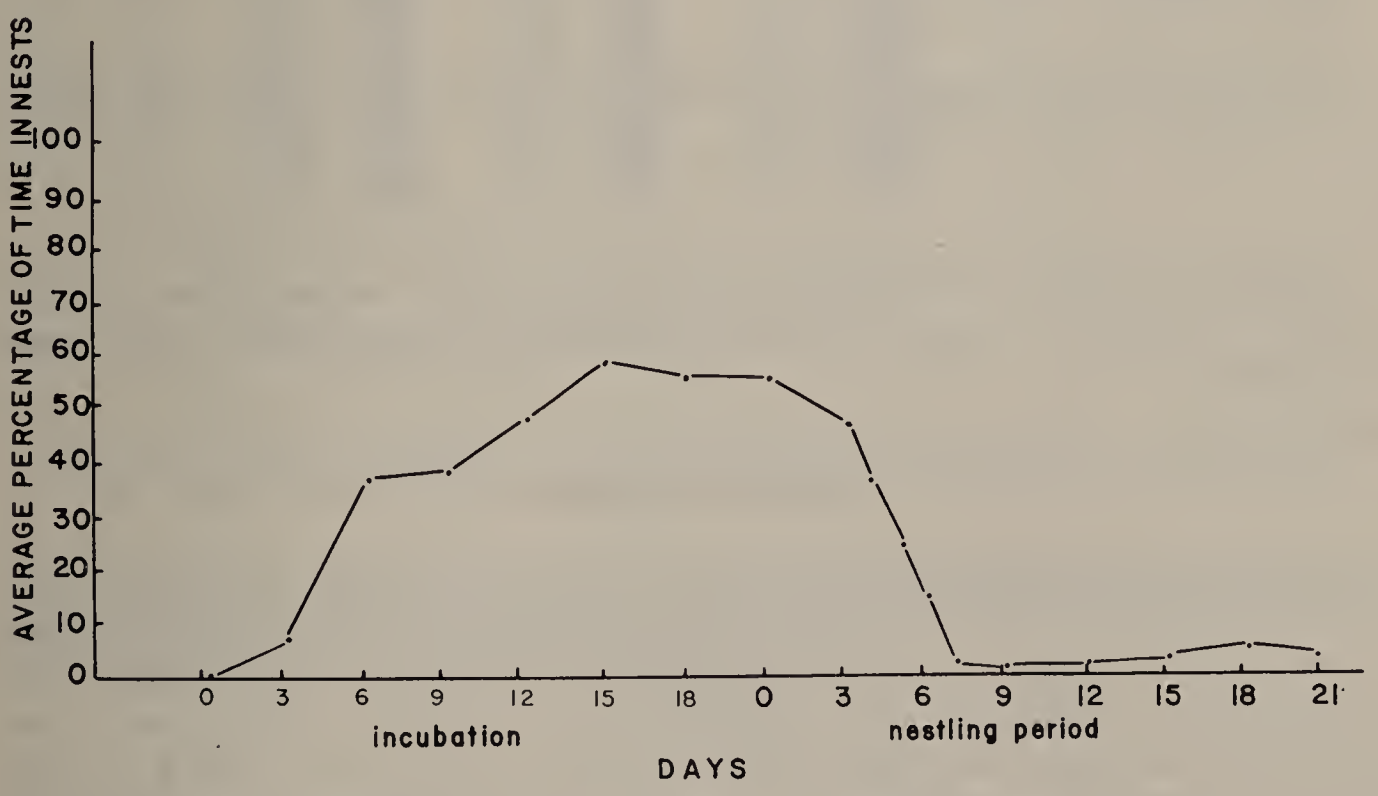


Fig. 10.5 Time spent by *T. mexicanus* inside burrows per visit during incubation and nestling periods. Data from 29 nests in Luquillo and Guánica Forests, taken during all types of weather in 1969 and 1970 (151.5 observation hours). Each point represents an average of eight to twenty-eight points over a three-day interval.

Duration of Visits

The attentive period during incubation is an average of 13.1 min, but after hatching the length of the visits progressively decreases by 4 min each day of the three successive days. The rate levels off to a quick 6-sec visit from the seventh day onward (Fig. 10.5; Table 10.2). Thus, during the whole nestling period the adults spend only approximately 2% of daylight hours in the burrow, giving the birds ample time to forage. If two nest helpers are present each adult spends less than 0.5% of the period of daylight inside the burrow.

This rhythm of attendance is typical of hole-nesters but not of cup-nesters (Fig. 10.2).

Daily Rhythm.—While the feeding tempo does not vary greatly during the day, the highest rate occurs in early morning and the lowest rate in late morning (Table 10.3). This is typical of many birds as, for example, the Blue-gray Gnatcatcher (Root, 1969).

TABLE 10.3

VARIATIONS WITHIN THE DAY IN NUMBER OF FEEDING TRIPS TO NESTS WITH TWO NESTLINGS [1)]
(six to nine days old)

TIME OF DAY	AVERAGE NO. FEEDING TRIPS PER NESTLING PER HOUR
Early morning (06:42 - 08:43)	8.5
Late morning (09:46 - 10:37)	3.0
Early afternoon (12:40 - 13:42)	5.5
Late afternoon (15:10 - 17:44)	5.7

1) Data from four nests during rainy or cloudy weather. Observations periods range from one to two hours each (N = 12.3 hrs)

Todies bring only one item of food per visit. The nestlings never waddle to the entrance to receive it as in puffbirds, woodpeckers, and some kingfishers.

Effects of Weather

Todies feed less efficiently in cloudy or wet weather (Chap. 6); one outcome of this is a decrease in visits to the nest (Fig. 10.6). At one nest during a particularly stormy week in May (530 mm of rain in eight days), the youngest of a brood of two, a day-old bird, starved to death and three days later the 5-day-old chick died. The latter had only reached a stage of development comparable to a 3- or 4-day-old nestling. The parents and helpers obviously faced difficulties in procuring food and this was reflected in the number of visits to the nest which were no more than 2/day.

Nevertheless, insect density in Luquillo Forest shows a four-fold increase during May (Kepler and Kepler, in prep.), so that despite the regularity

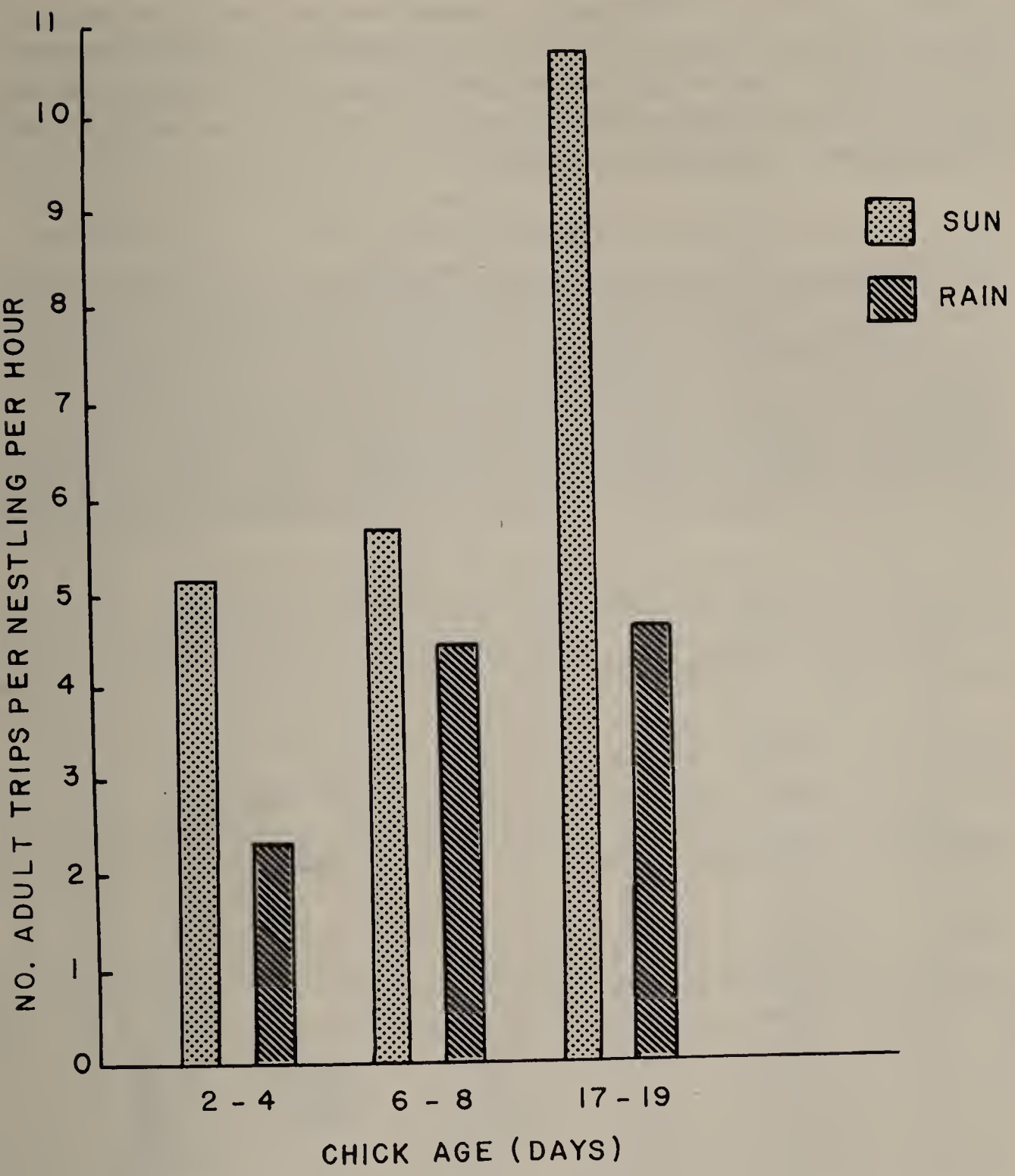


FIG. 10.6 Effect of weather on rate of feeding of nestlings of *T. mexicanus*. Data from 26 observations of 20 nests, taken from dawn to dusk (68 observation hours).

of unfavorable weather in this month, todies and other rainforest birds find food at its peak of abundance (Fig. 14.1).

DIET

While feeding their young, todies are surprisingly tame. They retain their "favorite perches" and often sit several minutes before entering their burrows, thus enabling me to identify and visually measure many of the food items with the aid of binoculars. In addition I collected the more easily recognizable prey and consulted insect collections for further identification. "Ringing"

the necks of chicks to collect insects, as has been performed on blackbirds (Orians, 1966 and Orians and Horn, 1969), was impracticable for burrow-nesting todies. Even though not precisely accurate, the following account and graphs present information on nestling diet and adult discriminatory foraging behavior (details in Appendix 3).

Types of Food

Of 295 identified food items, most of which were from the rainforest, 97% were insects and 3% spiders and nematodes (Appendix 3). Ten insect orders were recognizable, including 19 families; the five most common orders, comprising 89% of the nestling diets (Fig. 10.7), are considered below.

Homoptera (30.0%)..—Green lanternflies (Fulgoridae) and leafhoppers (Cicadellidae) comprised most of the Homoptera. They were brought in mostly after the young were six days old. Lanternflies are exceptionally

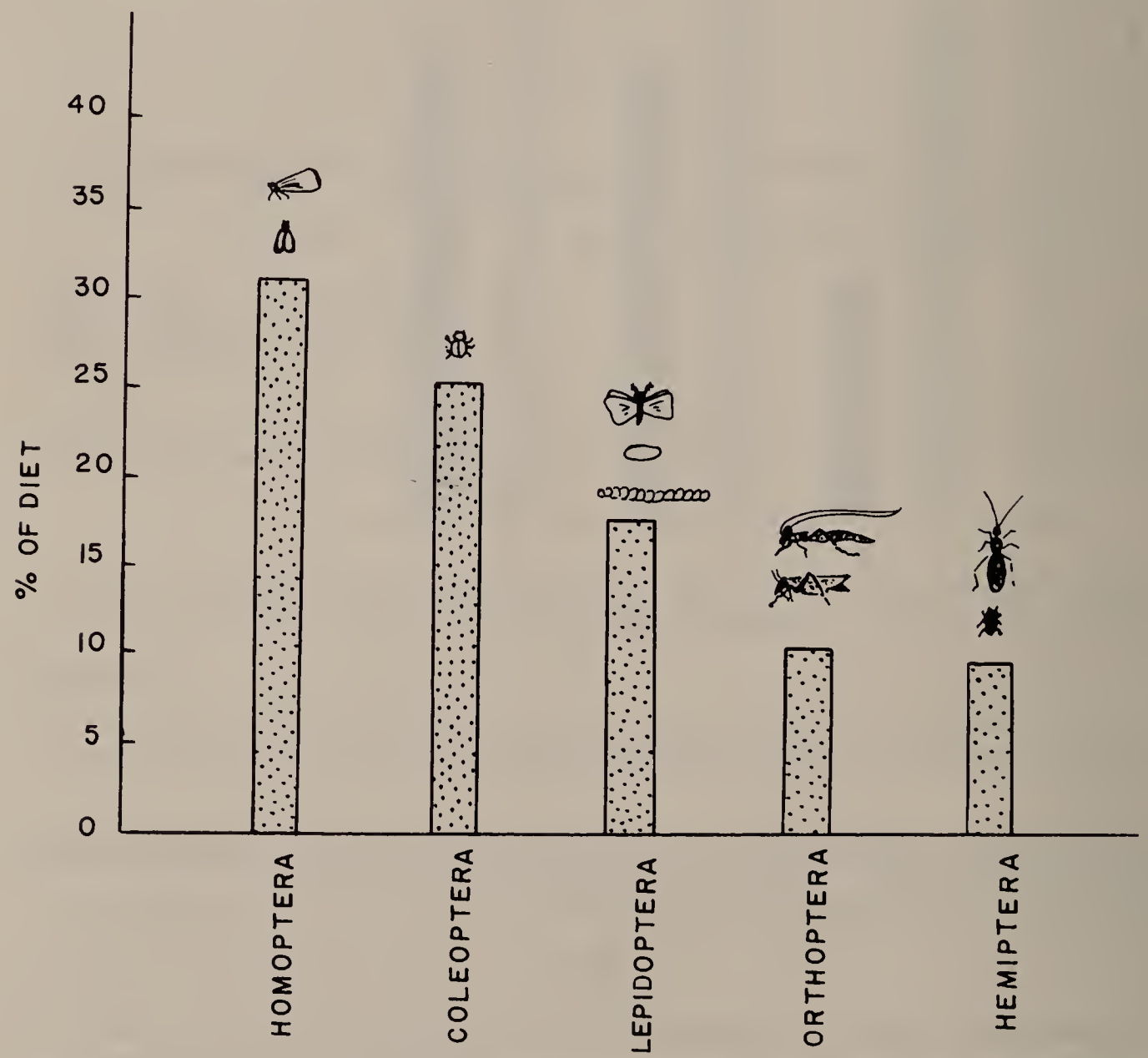


FIG. 10.7 Chief components in diet of nestlings of *T. mexicanus*. Data from 12 nests (mostly in Luquillo Forest), taken during 1969 and 1970. The five orders considered comprise 89.3% of the diet. N = 264 food items.

abundant in the West Indies (Drewry, pers. comm.).

Coleoptera (24.7%).—Beetles were important dietary items from hatching to fledging. They appeared to be chiefly fungus weevils (Platystomidae), ladybugs (Coccinellidae), and leafbeetles (Chrysomelidae), although some of the latter may have been long-legged flies (Diptera, Dolichopodidae), and other small, metallic green insects.

Lepidoptera (16.3%).—These were important food items after the sixth day and consisted primarily of green measuring worms (Geometridae), brown owlet moths (Noctuidae), and white tiger moths (Arctiidae).

Orthoptera (9.5%).—These distinctive insects, normally quite large, were brought mainly to older nestlings. I discerned four groups, (1) stout, brown, long-horned grasshoppers (Tettigonidae), (2) long-antennaed cavecrickets and green Agraecinine palmhoppers[1] (Gryllidae), (3) green and brown "typical" grasshoppers (Acrididae), and (4) green or brown stick insects (Phasmidae).

Hemiptera (8.8%).—I recognized only a few species of true bugs (mostly negro bugs, Cydnidae), but since many hemipterans resemble small beetles, my figures may be low. The minute ones were brought throughout the nestling period and larger, spindly-legged damsel bugs (Nabidae) after the sixth day.

Other Orders.—The Diptera (Craneflies, Tipulidae; flowerflies, Syrphidae; soldierflies, Stratiomyidae; and midges, Chironomidae) made up 3.2% of my samples, the Dictyoptera (cockroaches) 2.5%; the Neuroptera (lacewings) 1%; the Collembola? (springtails) 0.7%, and the Trichoptera (caddisflies), 0.3%.

My dipteran count is low; many dozens of tiny insects brought to nestlings, especially during the first few days, included unidentifiable flies and beetles. Flies are the most abundant insects in the rainforest; they accounted for over 50% of insects caught in Malaise traps (Drewry, pers. comm.) and on sticky-paper traps (Kepler and Kepler, in prep.). They are particularly abundant at night, but members of the common diurnal families such as the Mycetophilidae and Dolichopodidae, which are eaten in great quantities by adult todies, are probably fed to the nestlings.

Changes in Diet

Adult todies discriminate between the type and the size of food they bring to the nestlings, at least during the first few days of life (Figs. 10.8 and 10.9). In the beginning adults bring tiny flies, beetles, and bugs which are less than 3 mm in length; by the time the chicks are six days old they are fed items up to 15 mm in length. At this point, i.e., when the young themselves are 40 to 50 mm long, there is a sudden increase in the diversity of prey, and small grasshoppers, palmhoppers, cockroaches, moths, spiders,

[1]These belong to an undescribed genus and species (Drewry, per. comm.); I call them palmhoppers, as they typically inhabit undersides of palm fronds.

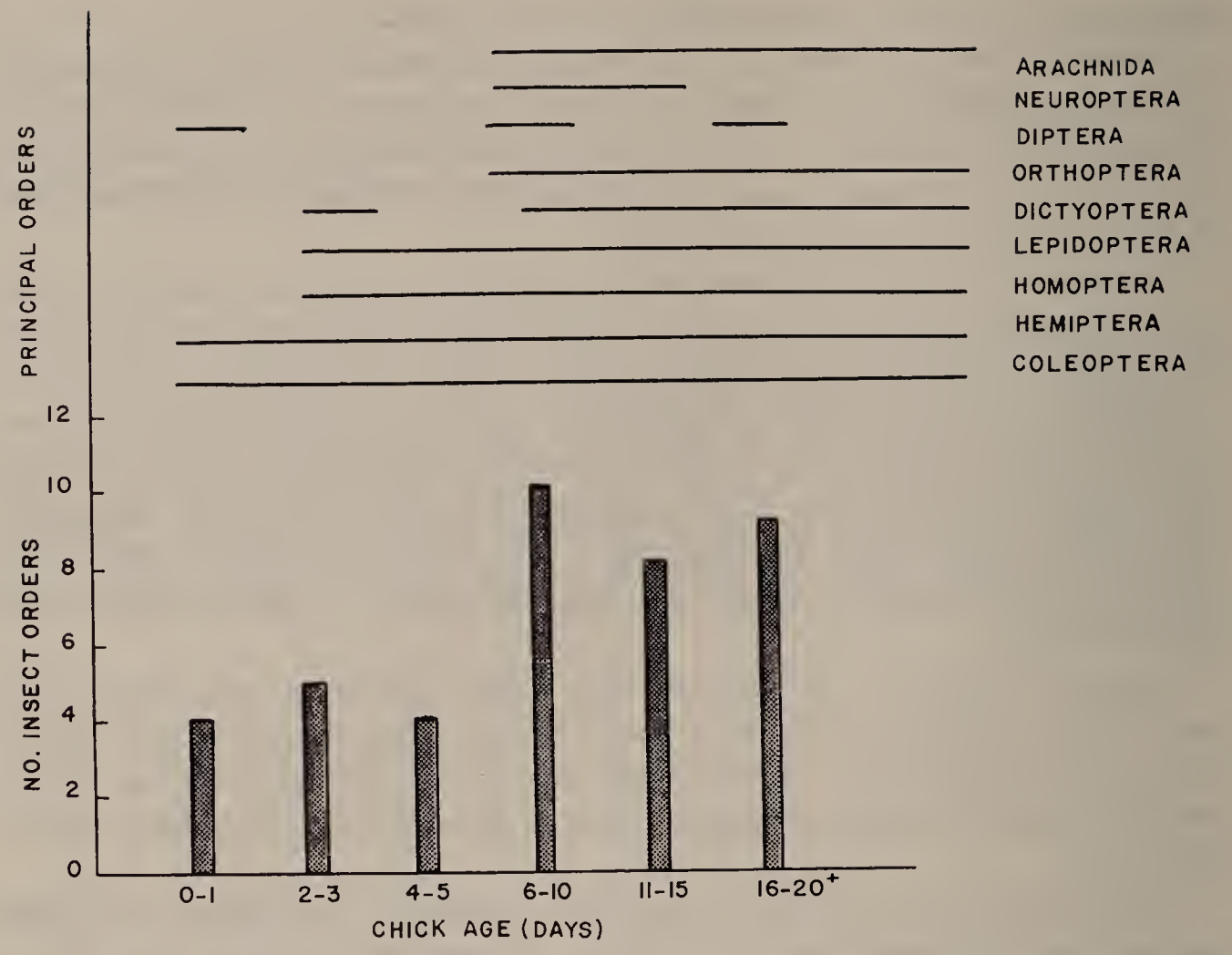


FIG. 10.8 Composition of nestling diets: insect orders as correlated with the age of nestlings. Data are from 12 nests (mostly in Luquillo Forest). N = 328 food items.

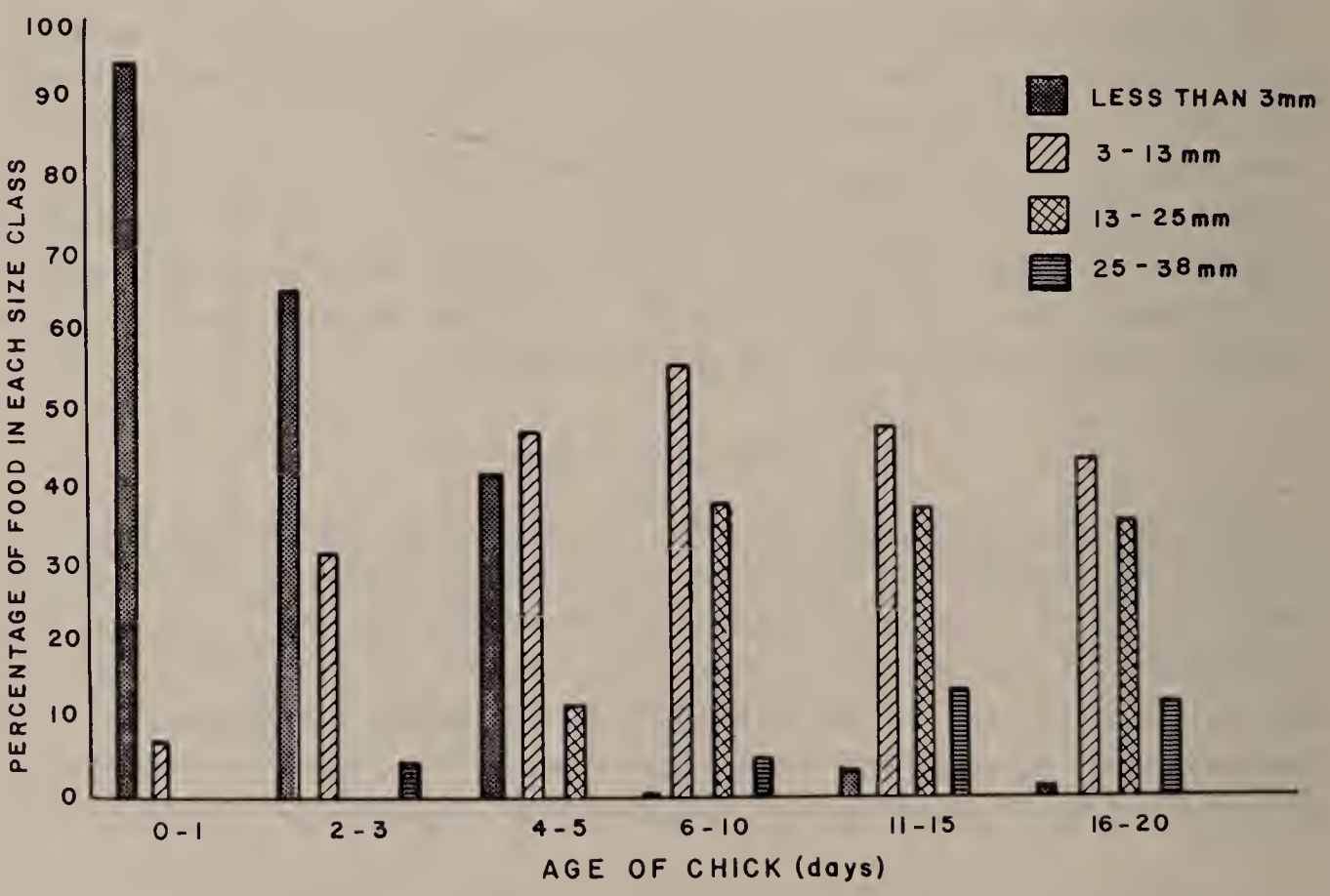


FIG. 10.9 Change in food size as related to the age of the nestlings. Data are from 12 nests (mostly in Luquillo Forest). N = 328 food items.

and lanternflies up to 25 mm are added to the diet. Soon chicks accept sizes and varieties of food up to 40 mm long, such as caddisflies, lacewings, soldierflies, stick insects, long-horned grasshoppers, stout caterpillars, and brightly-colored pupae. (For illustrations, see Kepler, 1972, fig. 10.10.)

The few studies available on the diets of hole-nesters generally give sketchy information on the food of the young, and usually consider it to be similar to that which is taken by the adults, e.g., House Wren, *Troglodytes aedon*, (Bent, 1964); and Roughwinged Swallow (Lunk, 1962). Tinbergen (in Lack, 1954: 131), studying tits (*Parus* spp.) in Holland, found that adults definitely did not hunt at random, but rather that there was a pronounced size selection and certain types of caterpillars were favored above others. However, over any short period, their prey was varied. Amazon Kingfishers also show "a nice discrimination in adjusting the size of the minnows to nestling capacity" (Skutch, 1957).

Nest Sanitation

Nest sanitation is not practiced by most Coraciiforms and other hole-nesters if their young do not form fecal sacs as, for example, the trogons and jacamars. With some kingfishers (*Halcyon, Megaceryle, Chloroceryle*) a potent smell of ammonia exudes from the nest hole, smarting the eyes, and liquid feces may ooze from the mouth of the burrow as flies buzz about and maggots crawl on the floor. On the other hand, the older young of other kingfishers (*Alcedo, Dacelo*) forcefully discharge their feces out of the tunnel, with the result that the burrow is somewhat cleaner (Bent, 1940; Skutch, 1957; Thomson, 1964). Todies, being insectivorous, do not rear their young under quite such unsanitary conditions, but, even so, by the time the nestlings are ready to fledge, their chamber is filthy, odorous, and sometimes invaded by insects (e.g., ants). However, despite their feculent nursery, the nestlings' plumage is clean and I was unable to find any external parasites in it.

Nest Helpers

Nest helpers are dealt with in detail in Chapter 12. In brief, at 11 nests where three or four different adults were positively identified, all helped, although somewhat erratically, to feed the chicks. Some of these same adults (36%) also assisted during incubation. In two broods studied, each of which was fed by four adults, the young were one or two days more advanced morphologically and behaviorally during almost the entire nestling period than were the young from nests with fewer attendants. In one group the eyes opened by seven days of age instead of at the usual 10 days; these young fledged at 17 days, two or three days earlier than usual.

Development

General

I did not study growth and development thoroughly because of the inaccessibility of the chicks, because of the probability of causing the nests

TABLE 10.4

MORPHOLOGICAL AND BEHAVIORAL DEVELOPMENT OF *mexicanus* NESTLINGS [1)]

		STAGE 1			STAGE 11	STAGE 111
Days:	0 - 1	2 - 4	5 - 7	8 - 9	10 - 12	13 - 20
	Bright pink, naked		Paler pink, essentially naked		Gray-green. Feathers dorsally; gray-white ventrally	
	Well-developed legs; heel callosities		Relatively well-developed legs; heel callosities		Relatively well-developed legs; callosities	
	No evidence of feather tracts	Anterior and ventral tracts and remige dots appear under skin	Blue-black pin-feathers on all tracts, mostly anterior. Ventral tract with yellow quills. Bare bellies and backs. Minute tails. Capital tract sparse.	As for 5-7 days; on day 9, beginning of green scapulars.	All pin-feathers have burst, although barely on remiges.	Remiges grow longer
MORPHOLOGY	Bill an equilateral triangle, slightly serrated tomia, hooked maxilla	Bill slightly longer	Hook disappears, serrations less obvious. Bill an isosceles triangle	Bill longer	Bill longer	Bill still less than half adult length
Length (mm)	7-9	up to 26	up to 50	up to 60	about 60	60-80
Weight (g)	-	-	3.6	-	-	-
Bill (mm)	up to 3	4-7	4-8	4-8	5-8	5-8
Tarsus (mm)	-	up to 8	8	10	10-12	more than 12
Wing (mm)	-	9	9-10	10-12	-	-
Tail (mm)	none	none	0-1	1-2	up to 14	14-15
	Egg-tooth present	Egg-tooth present	Egg-tooth disappears	Egg-tooth gone	Ditto	Ditto
	Helpless, sprawled with legs to side, pointing back	Sprawled, except head; body drags	Sits on flat tarsi, less sprawled. Supported by wings forming a triangle. Legs at right angles to body. Very uncoordinated.	Legs farther under body. Can lift body.	Quite coordinated	Coordinated
BEHAVIOR	No huddling, no wiggling	Wiggles	Huddling begins. Young move as a unit, especially towards light	Huddling present	Huddling normally stops	No huddling

1) See text for description of stages. Observations extend over three seasons from 35 nests.

to be abandoned, and because it would have interrupted the gathering of data on adult behavior around nests. However, whenever possible I recorded the growth and development of the behavior of young. This information is summarized in Tables 10.4, 10.5.

Development is a continuous process, although it is customarily divided into stages to facilitate description. Nice (1962) recognizes five stages in

TABLE 10.5

DEVELOPMENT OF SOME IMPORTANT CHARACTERS IN NESTLING TODIES

CHARACTER	DAY NO.	COMMENTS
EGG - TOOTH	0	At greatest development, used during hatching
	5 - 6	Disappears
EYES	0	Prominent blue-black protuberance, no slits
	3	Eyes sensitive to light, slits differentiating
	7	Slits barely opening
	10	Eyes open (in more advanced chicks, open at seven days)
FEATHERS	0 - 1	Body completely naked, no evidence of feather tracts
	3	Rudiments of pin-feather remiges breaking through
	7	Pin-feathers on all tracts, most developed at anterior end on humeral tract (scapulars) and ventral tracts; short stubby remiges
	8 - 9	Pin-feathers very long; bodies appear like miniature porcupines
	10 - 11	Sudden blossoming of green juvenal plumage as pin-feathers burst all over body
	19 - 20	Completely feathered, wings almost adult size
STANCE	0	Helpless, sprawled on belly; legs lateral, pointing backwards
	2	Head lifted up, rest of body sprawled, belly on ground
	4 - 5	Flops awkwardly; huddling begins
	6	Sits back on haunches, bill pointing slightly upwards. Large belly still heavy and mostly under legs; attempts to pull body up off ground; uncoordinated
	8	Body can be lifted off ground. Legs pulled farther centrally. Bill points 25 - 30° upwards. Beginnings of body control
	9	Wings can be held horizontally and folded back; flapping possible. Stretches neck, quite alert
	12	Huddling stops; can run and flap wings. Incipient flying behavior evident
	18 - 20	Sits most of time with body lifted off ground. Ready to leave nest and fly
VOCALIZATIONS	0	Silent
	3	Few, high-pitched, very faint squeaks
	5 - 12	Squeaks lower in pitch, becoming very loud and trilly
	13 - 20	Capable of trilling continuously for up to an hour. No evidence of adult Beeps, even on fledging day

altricial cup-nesting birds, which may be applied to todies, with slight alteration of periods. These are:

"I. Post-embryonic: first four days. Coordinations mainly concerned with nutrition; hearing present, but not sight" (0 to 9 days in todies).

"II. Preliminary: five and six days. Beginnings of comfort movements; eyes open" (10 to 13 days in todies).

"III. Transition: seven, eight, and nine days. Crouching; maturation of comfort movements" (13 to 19 or 20 days in todies).

Stages IV (Locomotory) and V (Socialization) are discussed in Chapter 11.

Heel Callosities

Cushioned heels, covered with a thick pad of swollen skin and numerous tubercles, are present in todies from hatching till fledging (Fig. 10.10). In either smooth or nodulose forms, similarly protective heel callosities occur in chicks of many species that pass their early development in unlined nests, whether in a soil burrow, tree hole, or termitarium cavity littered with tough,

Fig. 10.10 Calloused foot of nestling (× 4). Drawn from life (8-day-old nestling), specimens, and photographs.

irregular chips. Examples of these birds are motmots, kingfishers, woodpeckers, trogons, toucans, honeyguides, and some parrots.

Huddling

From about five to 12 days young todies usually huddle together in the center of their chamber with wings and heads interlocked, appearing as a single mass of fleshy pink balls. This behavior has been reported for Belted Kingfishers (*Megaceryle alcyon;* Bent, 1940: 115) and Black-chinned Jacamars (*Galbula melanogenia;* Skutch, 1937).

Characters Shared with Other Coraciiform Nestlings

Specific characters indicating Alcedine affinities are: absence of natal down, huddling behavior, a period of about three days for eyes to open fully

once slits appear, almost complete covering by contour feathers two-thirds of the way through the nestling period, and roughened tarsal callosities. Furthermore, I found that nestling todies have hooked bills and finely serrated tomia during the first six or seven days (adults possess microscopic bill serrations, *vide* Forbes, 1882; Sibley, 1955). This last character, plus numerous additional morphological and behavioral features, seem to link todies more closely with motmots than with kingfishers (see Kepler, 1972, tables 1.4–1.6, figs 10.14). There is also a striking resemblance in posture and pterylosis between adult todies and Tody Motmots, and young fledgling Turquoise-browed Motmots (*Eumomota superciliosa*). (See Chap. 15.)

11
JUVENILES

Fledging

When nearing fledging, the nestling ventures a short way down the tunnel, forcing adults to back out if they enter. Soon the young bird's whole body is visible at the entrance. The bird Wing-flicks and moves its legs and body continuously, while squeaking approximately once per second. Nestlings emerge singly after repeated retreats to the nest chamber, during which time the adults feed them constantly, vocalize loudly, and hover in front of the entrance hole. The young generally fledge within 24 hours of one another.

A behavior commonly used by birds to terminate the nestling stage is to reduce feeding, but in todies the number of feedings generally *increases* during the last few days in the nest (Fig. 10.4). Two or three days before fledging, adults of *T. mexicanus,* usually carrying food, hover at the nest hole. They Beep, eliciting trills and squeaks from the chicks, but do not enter; they may return quickly to their "favorite perches" or resume feeding nearby. Later the parents (and helpers if present) become extremely agitated, Bobbing and Beeping almost continuously, their calls accelerating as they intersperse Loud Beeps and Bee-beeps. Loud trills are rendered by the chicks.

Skutch (1953) discusses the ". . . widespread belief among ornithologists that young birds generally quit the nest in response to the urgings of their elders. . ." He believes that records of apparent coaxing are the result of observers having frightened the adults and then having misinterpreted the significance of the behavior of the alarmed birds. Some of my observations may have been of alarmed birds, although twice I was *attracted to* nest sites by commotion created by the adult todies.

In contrast to some hole-nesters, such as wrens, young todies never return to their nests, even during the night. I watched one chick roost on two consecutive nights. About 6 hr after fledging and 1 hr before nightfall, its parents led it up to foliage at 11 m (canopy 13m), where it remained huddled and clinging to a perch 5 mm in diameter and only 10 m from its burrow. The following night its last meal was 40 min before dark and, after much squeaking, it slept 8 m up in a tree, 12 m from the burrow.

Developmental Stages

The first three developmental stages (immobile) of Nice (1962) (I, Post-embryonic; II, Preliminary; III, Transition) have been discussed in Chapter 10. The next two stages, which I have arbitrarily split into four (Table 11.1, Fig. 11.1), are: "Stage IV. Locomotory. Leaving the nest, start of self-feeding; 10 to 16 days" (about 19 to 27 in todies) and "Stage V.

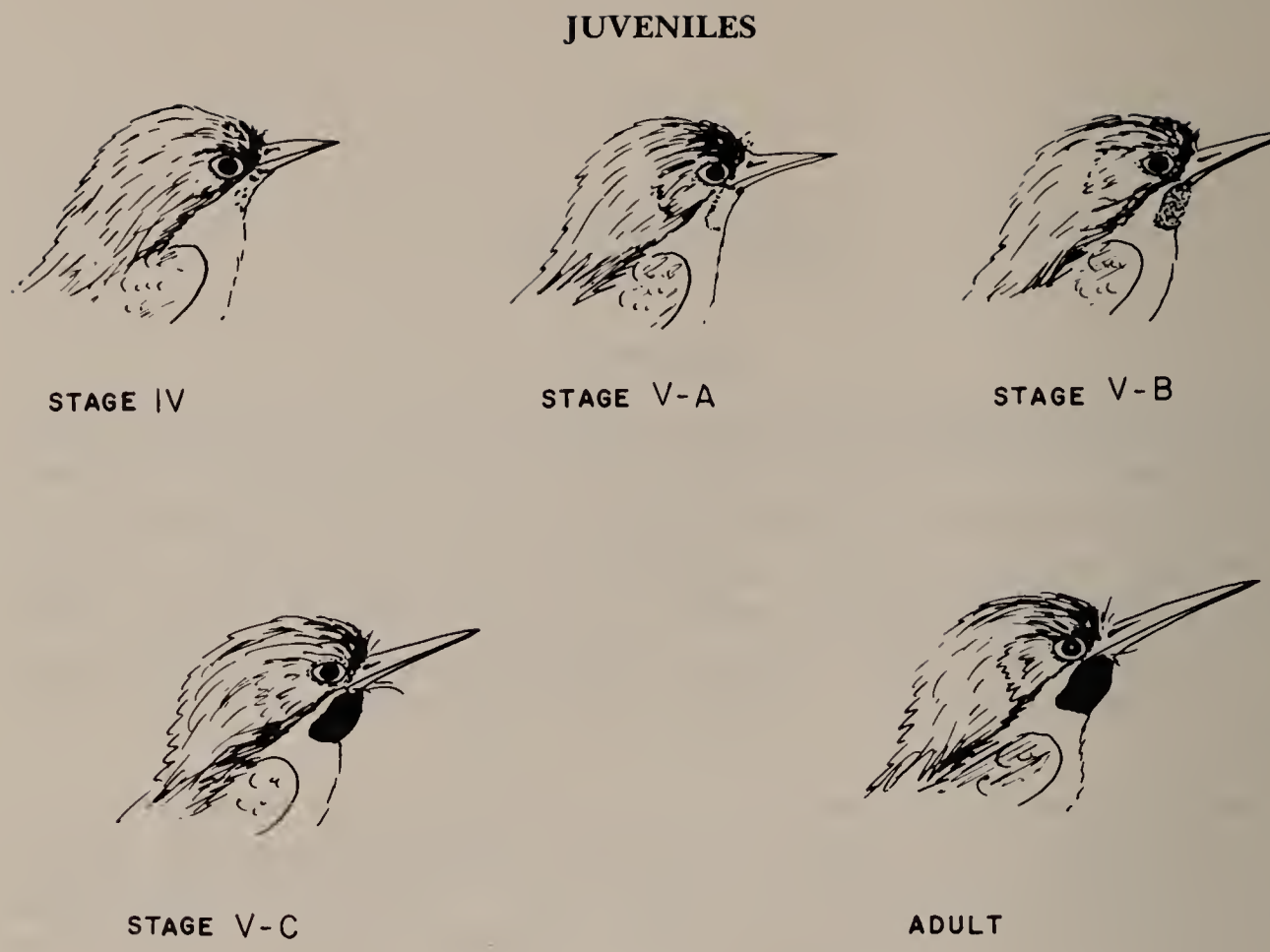


FIG. 11.1 Juveniles (*T. mexicanus*) in four stages of maturation, showing changes in bill and bib morphology and degree of bill-tilting. Light shading indicates a pale pink bib; darker shading is a darker pink merging into scarlet.

Socialization. Aggression, flight, perfection of self-feeding; 17 to 28 days" (about 28 to 42 onwards in todies).

FEEDING

I watched 16 families of *T. mexicanus* feeding in all habitats, but mostly in scrubland; observation periods ranged from a few minutes to eight hours.

Upon fledging the chick is fed almost immediately. The parents become the sole source of food as the helpers soon dwindle away. They are most attentive during early morning and late afternoon, feeding the young in concentrated bouts. After Stage IV no pattern was apparent.

When only one chick is present the female stays close and feeds it while the male remains a few meters away, usually in a different tree, chasing predators. Occasionally he even prevents the female from feeding the chick. If two chicks are present each adult cares for one, although the male also continues to chase potential predators. Males forage higher in trees than do females and chicks.

The insects and spiders fed to juveniles are essentially of the same variety and size as those given during the last few days of nestling life. They include Sphinx moths, caterpillars (Lepidoptera, Sphingidae), moths (chiefly Noctuiidae and Arctiidae), palmhoppers, grasshoppers, and crickets (Orthoptera, Gryllidae, and Acrididae), cockroaches (Dictyoptera, Blattidae), lanternflies

(Homoptera, Fulgoridae), craneflies (Diptera, Tipulidae), and soldierflies (Diptera, Stratiomyidae).

During Stage IV, while still dependent on the adults for food, the juveniles squeak often. If the adults have difficulty in locating the young, they utter a few sharp Beeps and Beep–trills, to which the chicks then respond. Twice in xeric scrub I heard a peculiar adult guttural sound (Guttural Feeding Call; see Chap. 3) when one parent was feeding its chick.

Behavior Leading to Independent Feeding

Immediately after the young fledge, the adults perch beside them, lean over, and poke food down their throats. But as early as the fourth feeding after fledging, the parent holds the food several centimeters away, requiring the chick to lean forward to grab it, the method continued thereafter. The parents varied this feeding behavior in several ways: (1) An adult with food lands within 20 cm of a chick but does not feed it, and soon flies off. (2) Adults hover about 10 cm in front of a juvenile, or land beside it, withdrawing food several times as the chick reaches to grab it. Finally, they either give the insect to the chick, swallow it themselves, or fly away with it. In most cases the young try to follow, sometimes in a very uncoordinated fashion. (3) An adult with food lands about 1 m from its offspring, requiring the latter to move actively to take the insect. (4) Adults (generally males) frequently fly rapidly at chicks, Wing-rattling, and appearing to push them off their perches, forcing them to fly. This behavior appears as early as day 20. At other times adults merely fly very close, Wing-rattling, and elicit a following response. Often the male chases both its mate and the chick prior to feeding, thus preventing the exchange of food. (5) On a few occasions adults land with live insects, instead of dead ones, immobilizing them on perches close to their chicks. Later these same adults may bring live insects for the young to kill, but I never saw these two events performed successively.

Comparison with Other Birds

There is a paucity of field studies on the development of fledgling behavior and adult "instruction" in atricial birds. Among Coraciiforms, White-fronted Nunbirds (*Monasa morphoeus*) in Costa Rica always hold immobilized insects in their bills and wait for the juveniles to fly up to catch them without alighting, a method perfectly suited to motionless perching interspersed with sallies of rapid activity, a characteristic of puffbirds (Skutch, 1969). Bent (1940) recounts a female Belted Kingfisher catching fish, beating them to partial insensibility, then dropping them into a pool where they were retrieved by the juveniles.

Development of Feeding Behavior

The development of refined feeding coordination may be followed from Table 11.1; within six weeks juveniles feed with the coordination, efficiency, and rate of adults.

TABLE 11.1

MORPHOLOGICAL AND BEHAVIORAL DEVELOPMENT OF *mexicanus* FLEDGLINGS [1)]

	STAGE IV (19 to about 27 days)	STAGE V-a (about day 28 to 36)	STAGE V-b (about day 37 to 41)	STAGE V-c (about day 42 on)
MORPHOLOGY				
Bib	Pale gray, plain or with blackish streakings	Very pale pink, mostly around edges	Pink, covers most of bib area	Darker pink, merging into red; complete
Bill	About half adult length, mandible pink	Longer	Longer	From almost adult size to maximum length
Legs	Pink	-	-	Gray
Tail	Tiny	Longer	Longer	Adult size
Flanks and Belly	Pale yellow	Pale yellow	Belly has new gray-tipped feathers; flanks bright yellow	Ditto
FEEDING RATES BY ADULTS	day 19-21: Up to 28 feedings/hr day 24-27: Up to 18 feedings/hr	Much less, very sporadic	Virtually none; zero to less than 2 feedings/hr	None
INDEPENDENT FEEDING	day 20: First attempt seen, a lurch forward from perch day 23-24: Flutters small distances from perch to capture insects crawling on leaf edges. Pecks at leaves while perched. Occasional Leaf-feeding, usually unsuccessful	Sidles along perch, reaches over to glean from leaf-tops. Flutters to leaves, awkwardly finding new perches. Much better at Leaf-feeding. Attempts to Air-feed. Improves rapidly. Can swoop down to leaf-tops in later stages. Two young were 60% successful, feeding once every 4-5 flights. Sometimes return to same perches. Foraging behavior still rather clumsy, cannot "judge" distances well or "pre-plan" landing locations.	Good feeders, plenty of confidence, but less adept than adults. Much Leaf-feeding, usually successful. Feed once every two or three flights. Can hover; feeding flights averaged less than 1m	Feeding indistinguishable from adults. One leans over and catches flying insect within 5cm of perch. Complete independence.
FLIGHT LENGTHS	day 19: After 20 min, can fly 10m across road. After 1.5 hr, less wobbly and shaky, flying 0.5 to 1m after each feeding from adult, increasing to 2.5m in next few days	Can fly in all directions, in straight and arched paths. Some fluttering. Average flight length 0.7m. First feeding flights shaky. Begins to hover.	Longer flights. No more fluttering. Almost complete co-ordination.	Complete co-ordination. Flight lengths like adult.

TABLE 11.1 (CONTINUED)

STANCE	day 19: Clings rigidly to perch, abdomen rests on branch. Within 20 min, body flicks upwards, shakes, peers around. After 1.5 hr, much more alert. Bill horizontal. day 20: Sits straighter, legs can be seen under abdomen. Turns clumsily on perch. Bobs first seen. day 21: More alert, space between legs and perch larger. Bill tilted slightly upwards. day 22: Greater alertness. Responds to shadows and movements and sounds nearby, by twitching and turning head. days 23 on: Cocks head more. Looks downwards carefully. Turns well on perch.	More alert. Much scanning, as head moves up and down and around. Each time it lands, looks all around, turns well on perch. Much silent Bobbing, especially as days progress. Much time spent with slightly upward-directed bill.	Very alert. Much silent Bobbing. Most of time sits with slightly-cocked bill.	Extremely alert, like adult. Bill at 40-45° angle most of time.
MAINTENANCE ACTIVITIES	day 19: One tucked its head and bill into dorsal plumage and Bill-wiped 2 hr after leaving nest. day 20: Vigorous preening, mostly underwings and flanks. First stretches wings, shakes body and fluffs. day 21: First Wing-flick, head-scratch, tail-fan and leg-stretch.	None seen	None seen	Indistinguishable from adults
VOCALIZATIONS	day 19: In first 1.5 hr, trills most of time, then squeaks less, usually when hungry or left alone for night only. day 20 on: Squeaks periodically, even while feeding itself.	Baby squeaks still present. Some guttural sounds. Attempts to Beep, high-pitched. Low Beeps like Muttering serve as hunger calls.	Baby squeaks gone. Much Beeping, still high-pitched. Some sharp Beeps.	Beeps indistinguishable from adults. Loud Beeps take over 6 mths to develop correct pitch. Wing-rattling is present at 4 mths.
MISCELLANEOUS PARENTAL CARE	Adults lead young to treetops to sleep for at least two days. Adults chase predators, stand guard closeby; begin "pushing" young off perches and using other devices to teach young independence.	Family still together, male guarding while female feeds young, or each sex cares for young (if more than one).	Ditto. Family not as close.	Parents may or may not be nearby.

1) See text for description of stages

JUVENILES

TABLE 11.2

DEVELOPMENT OF FEEDING BEHAVIOR IN CUP- AND HOLE-NESTERS [1)]

	HOLE-NESTERS		CUP-NESTERS	
	Tody	Passerines	Song Sparrow	Blue-Gray Gnatcatcher
Leave nest (no. days old)	19 - 20	15 - 20	10	13
Moves little, hides in undergrowth	passed during nestling stage			14 - 17
Exploratory pecking	21	-	12	22
Catches some of own food	24	28	16	23
Bulk of food from adults	19 - 27	up to 60	10 - 21	13 - 26
Catches part of own food	about 30	up to 60	22	29
Occasional food from adults	about 39	up to 60	23	33
Completely independent	about 43 (i.e. 24 days after fledging)	up to 60	28 (i.e. 18 days after fledging)	34 (i.e. 21 days after fledging)

1) From Nice (1937), Root (1969), Skutch (1953) and this study.

On comparing todies with other birds (Table 11.2), we see that all hole-nesters spend longer in the nest than do cup-nesters (see, also, Chap. 10), that fledgling todies begin exploratory foraging almost immediately while cup-nesting young may not attempt this for more than a week, and, finally, todies attain independence later than do cup-nesters. This is as expected. On account of the todies' specialized feeding, one would expect them to take longer to perfect the technique than would be needed, for

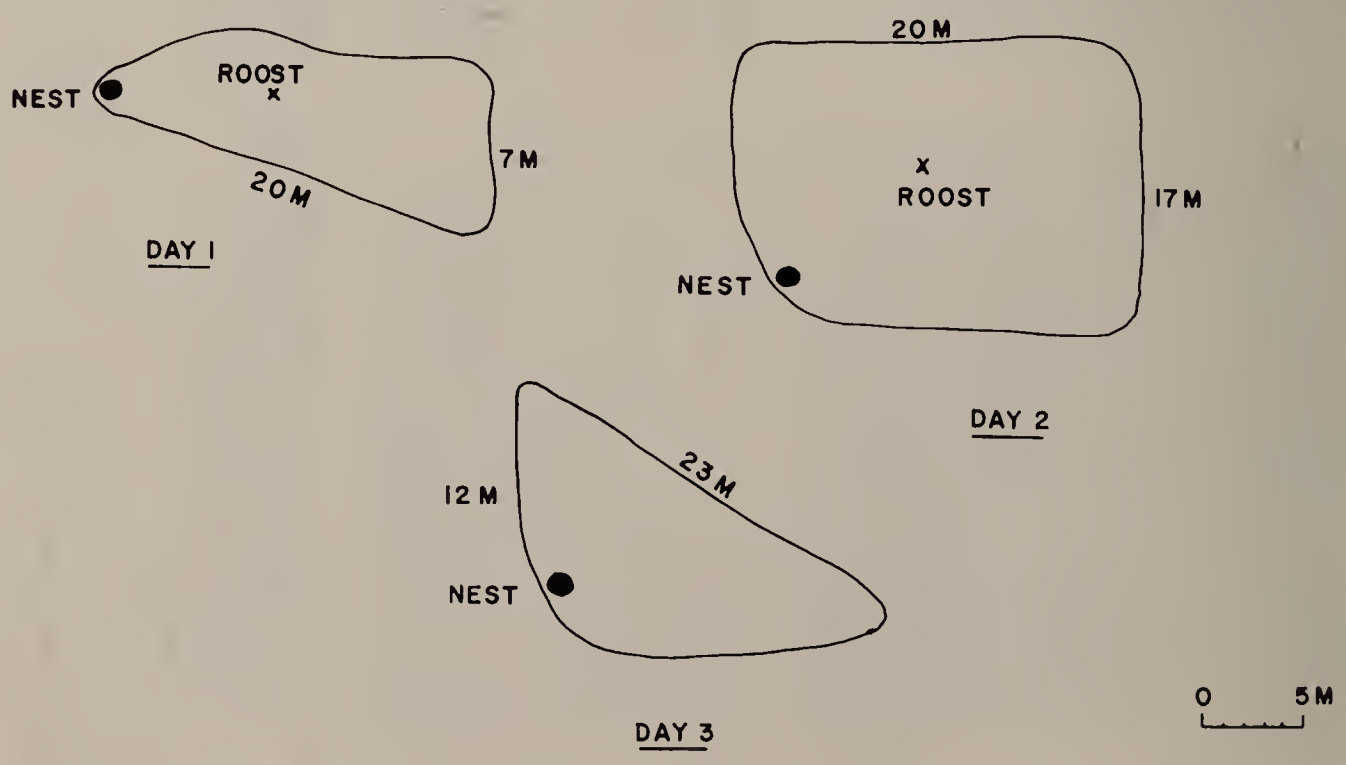


FIG. 11.2 Area covered by one *T. mexicanus* fledgling in its first three days after emergence, Luquillo Forest, Tabonuco Zone, 1969.

instance, by a simple leaf-gleaner. Note that the aerial-feeding gnatcatcher (*Polioptila caerulea*) spends more time learning to feed than does the Song Sparrow (*Melospiza melodia*).

Expansion of Feeding Area

In the rainforest I followed the movements of 10 juveniles from five nests for periods ranging from 15 min to two weeks. During Stages IV and V-a none of the birds ventured farther than 25 m in any direction from the nest site. The area encompassed by one tody in its first 3 days is mapped in Figure 11.2.

I have no information on the length of time fledglings reside within their parents' territory; after 3 months all banded young had disappeared. This was undoubtedly due to mortality, my lack of knowledge of precise home ranges, difficulties in sighting birds, and emigration.

12
NEST HELPERS

A "helper" is a bird that assists in the nesting of an individual other than its mate, or feeds or otherwise attends a bird of whatever age that is neither its mate nor its dependent offspring (Skutch, 1961).

About 160 species of birds, from pelicans to finches, have been found to have helpers that aid in feeding young, nest building, incubation, or caring for injured birds (Skutch, 1935, 1961; Fry, 1969, 1972; Harrison, 1969; Woolfenden, 1975). Helpers appear most frequently among birds whose eggs and young are somewhat inaccessible, being contained in holes, or are in hanging nests; they also are found among farly large and aggressive cup-nesters such as the jays.

In addition to the Todidae there are 12 other families of hole-nesters that have at least one species with "helpers", viz., Artamidae, Bucconidae, Certhiidae, Hirundinidae, Meropidae, Upupidae, Phoeniculidae, Picidae, Ramphastidae, Sittidae, Troglodytidae, and Turdidae. Among the bank-nesters, besides the todies, the phenomenon is found in the Bank Swallow (*Riparia riparis*) and in several species of *Merops* bee-eaters. The todies constitute the fourth family with "helpers" within the Coraciiformes.

My information on todies is incomplete, being based on relatively small samples and few banded helpers, but I present it in the hope that someone may later fully investigate the phenomenon. Pertinent figures are presented in Table 12.1.

Behavior

Supernumerary adults are not obligatory. In the rainforest 48% of 23 closely-studied nests had three or four attending adults. In xeric scrub none (or possibly one) of five closely-studied nests had helpers. This order of frequency seems to be in the general range of occurence in other avian taxa.

Although few species with helpers have been adequately studied, Rowley (1965) found that in the Australian Blue Wren (*Malurus cyaneus*), less than half the breeding pairs possessed helpers, and Woolfenden (1975) noted the phenomenon in about half of all paired Florida Scrub Jays, *Aphelocoma coerulescens*.

When tody helpers are present, they assist only sporadically; such erratic attention has also been observed in Australian passerines (Harrison, 1969) and is undoubtedly why many instances of intraspecific nest helpers have been overlooked. Helpers do not seem to play a role in the excavation of tody nests; I never saw more than two adults at work on a burrow. Incubatory helpers, even though present in 36% of helped nests, and although they appeared as early as the fourth day, were of immaterial practical help. On the other hand, helpers were active during the nestling period in all

TABLE 12.1

COMPARISON OF NESTS WITH AND WITHOUT SUPERNUMERARY HELPERS

	WITH HELPERS	WITHOUT HELPERS
No. nests with complete data	11	6
No. nests with helpers during incubation only	4 (36%)	7
No. nests with helpers during nestling period	11 (100%)	0
No. successful nests	5 (45%)	3 (50%)
Total no. adults at successful nests	18	6
Total no. eggs laid in successful nests	14	7
Average clutch size [1]	2.9	2.0
Average no. young fledged per nest [1]	2.6	2.0
Total no. young fledged	13	6
No. fledglings per adult	0.72	1.00
Nestling period (days)	17 [2]	19

1) $0.05 > p > 0.025$, $\chi^2 = 6.19$

2) 2 nests

nests, contributing consistently, but in varying degrees, to the welfare of their foster chicks. When not continuing attendance which had begun at incubation, helpers appeared at any time up to the sixteenth day of the nestling period. At one nest four adults fed three almost fledged young at the greatest rates recorded in this study. Average feeding rates at hatching are 5 feedings/nest/hr, increasing to 27 at fledging; but 35 feedings/nest/hr for the two days before and during fledging were recorded when there were two helpers in addition to the parents. Although unbanded, these four adults were clearly recognizable. The presumed parents made 62.5% of the visits and the helpers 37.5% of the visits during the 13-hr observation period.

I do not have adequate data on sex ratios, but certainly both sexes assist. In the above example the parent female-male ratio was approximatley 16:14, and that of the helpers about 4:14. Helpers of both sexes are present in birds such as the Southern House Wren (*Troglodytes musculus*) and the Red-throated Ant Tanager (*Habia gutturalis*), where young of the first brood help raise the second brood. In the Brown-headed Nuthatch (*Sitta pusilla*) pairs that fail to breed will then feed nestlings of neighboring pairs (Skutch, 1961). The latter situation probably is similar to that in todies (see below).

Many species feed each other's young or assist in other ways merely because of social habits or nesting proximity, as for example, among the colonial swallows (*Petrochelidon, Riparia*), some wrens (*Heleodytes, Campylorhynchus*), and some babblers (*Turdoides*) (Skutch, 1935, 1961; Gaston, pers. comm.; Wilson, 1975). However, the situation with the todies is quite different because todies are territorial and nest singly, with no apparent social behavior either in or out of the breeding season. On many occasions resident todies at first prevent helpers from entering their territories or nest holes, but after

a few days their aggression abates. Such behavior has been noted in many other species (Skutch, 1935, 1961).

Clutch Size and Nest Success

In his review of nest helpers, Skutch (1961: 208) said ". . . no species that I know lays more eggs than one would expect from its systematic position and environment because of the fact that helpers are available."

Although the mechanism is puzzling, my data suggest that nests with helpers contain significantly larger clutches than nests without helpers (2.9 and 2.2 eggs, respectively). It may be questioned whether the nests with helpers are not merely successful ones rather than more productive nests, but the following data suggest that this seems unlikely: mean clutch of *all* nests (successes and failures), 2.4 (N = 44); mean clutch of all successful nests, 2.3; mean clutch of helped nests, 2.9; mean clutch of unhelped nests, 2.2.

Similar to the enhanced clutch size of aided nests, the average number of young fledged per aided nest was 2.6 compared to 2.0 in unaided nests. In Blue Wrens, Rowley (1965) showed that aided nests produced more young *per adult* than normal, although recent reanalysis of these data refutes this (Gaston, pers. comm.). In todies, where helped nests fledge 0.72 young per adult, as opposed to a normal 1.00, this situation is not present.

In the previous section we discussed the qualitative behavioral aspects of helpers during egg and nestling stages. The following data indicate that the contribution of helpers during incubation is negligable, but may be quite considerable during the nestling period, e.g., fledging success in nests with incubatory helpers only is 45% (N = 4); fledging success in nests with nestling helpers only is 75% (N = 8); and the overall success in nests with and without helpers is but 50.5% (N = 44).

Preliminary observations also indicate that nestlings mature more rapidly and fledge sooner when extra adults have assisted in their upbringing. For example, in one nest, the chicks' eyes opened at seven days instead of the usual 10, their complete feather covering blossomed two or three days earlier than usual, and they fledged at 17 days instead of the normal 19 or 20.

Identity of Helpers

I do not know the relationships of helpers to nesting adults, but evidence appears to indicate that they are *not* yearlings that have remained in their parents' territory since the last breeding season, which is a common phenomenon in many other species (Skutch, 1961; Wilson, 1975). Support for this statement is derived from the fact that territories contain only two birds, resident todies initially prevent other todies from entering close to their burrows, and helpers do not assist with burrow excavation but appear during late incubation and in the nestling periods. In addition, Guánica is a scrubland "saturated" with todies defending small territories. It contains very little marginal land into which juveniles can expand, with the result

that one would expect there to be great pressure for the young to remain with their parents. If nest helpers are yearlings, one would expect many more helpers here than in the rainforest, where marginal land is plentiful and tody territories are not contiguous. Preliminary observations indicate that, contrary to expectations, helpers are rare or absent in xeric scrubland.

The explanation most consistent with existing information is that these nest helpers are adults from nearby whose breeding activity was curtailed for some reason, or that did not breed at all. As todies rarely raise second broods (especially after March), it seems natural for suppressed breeders or unpaired "floaters" to attach themselves to nearby nesting pairs. This occurs in Brown-headed Nuthatches, *Sitta pusilla* (Skutch, 1961), Blue Wrens, *Malurus* spp. (Rowley, 1965), and other species.

From an evolutionary viewpoint, all that would seem necessary to develop this behavior would be the selection of a genotype to accept helpers. In the rainforest a number of advantages seem to have accrued to those accepting helpers. For example, clutch size is increased because more young may be fed and fledged, the nestlings fledge earlier, and the territory is better defended.

13
GENERAL ANALYSIS OF THE BREEDING SEASON

Information from over 600 burrows and families of the Puerto Rican Tody, discussed in detail in Chapters 7, 9, 10, 11, 12, and 14, is briefly considered in this synthesizing analysis.

Annual Reproductive Cycle

In the rainforest twelve months elapse from the time todies begin excavation until the last fledglings are independent, but actual breeding is concentrated

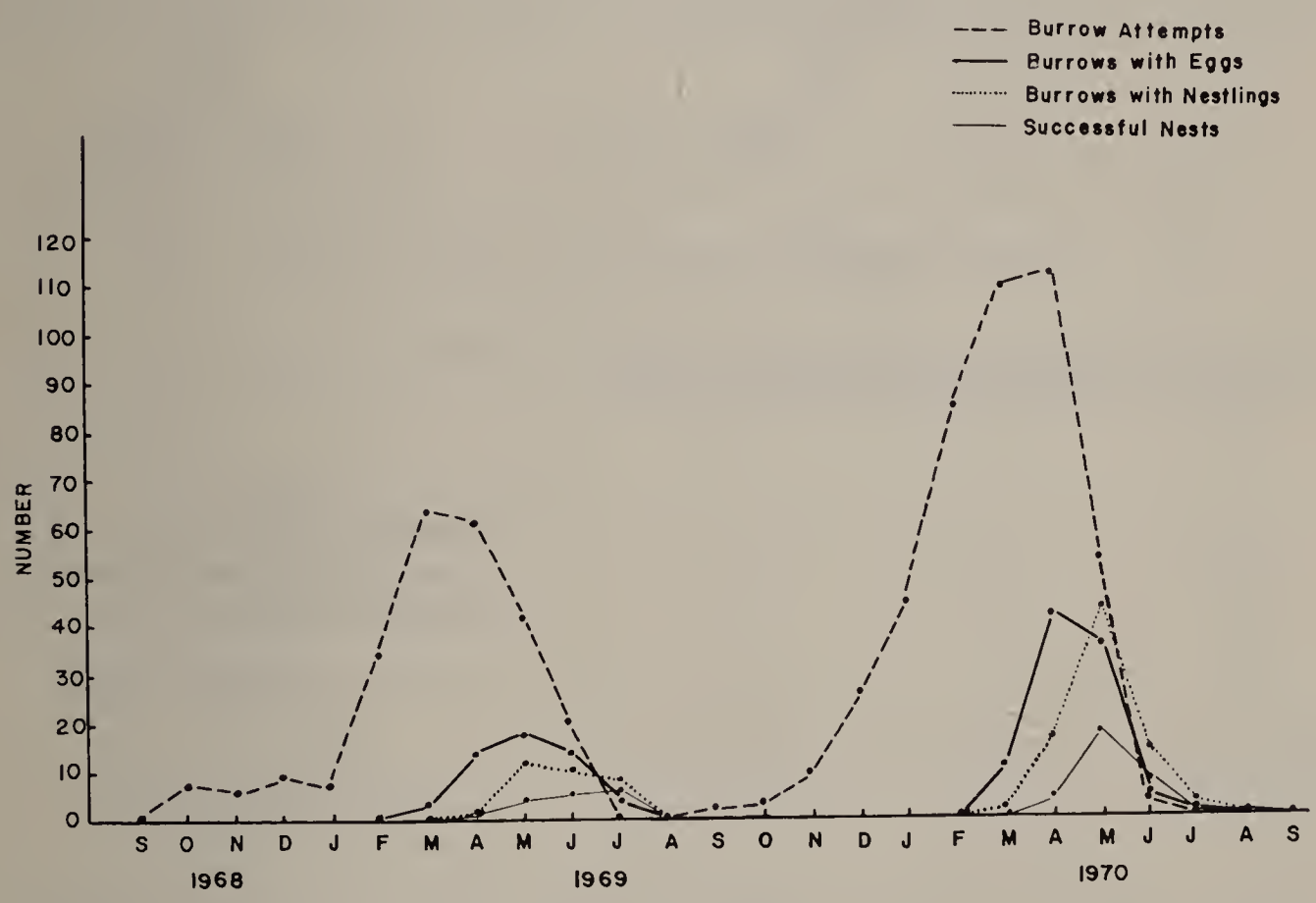


Fig. 13.1 Reproductive cycle of *T. mexicanus* in Luquillo rainforest. Data are from 492 fresh burrows, studied from 1968 to 1970.

from January through July (Fig. 13.1); in the dry scrub breeding occurs only in these months (Fig. 13.2). Such prolonged reproductive activity is typical of many tropical birds in the absence of severe climatic, food, or migratory pressures (Lack, 1952).

In 1968–1969, a "normal" season, the majority of nests were built from March to May, the peak egg laying month was May, nestlings were most frequent in May and June, and fledglings were commonest in July.

Generally a period of two weeks separates breeding peaks in Luquillo and Guánica. A serious drought in the spring of 1970 accelerated breeding readiness in rainforest todies but retarded it in the population in the scrubland,

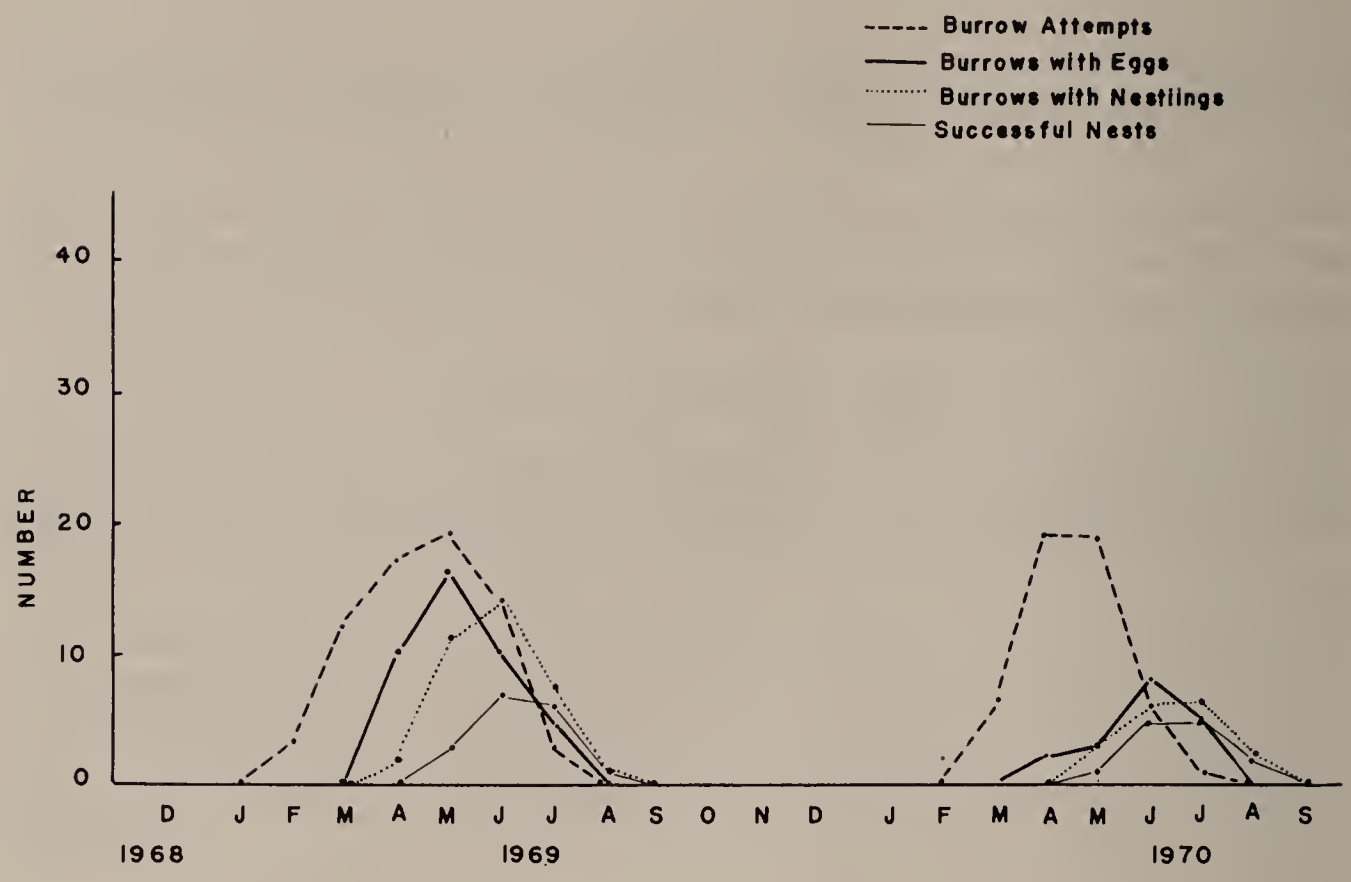


FIG. 13.2 Reproductive cycle of *T. mexicanus* in Guánica xeric scrub. Data are from 87 fresh burrows, studied from 1968 to 1970.

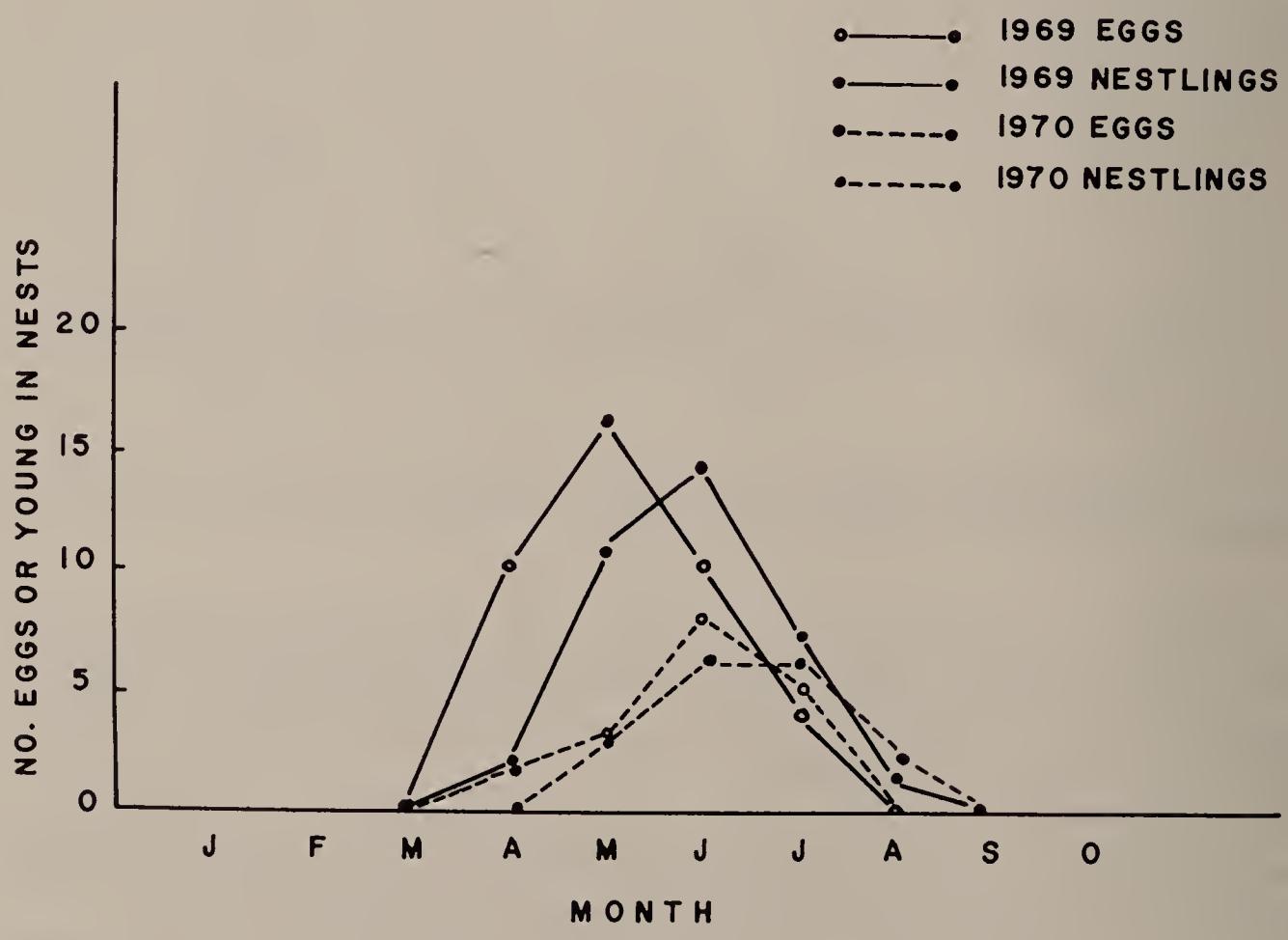


FIG. 13.3 Shift in peak breeding activity in Guánica during the 1970 spring drought. Data are from 87 nests, studied from 1968 to 1970.

resulting in a seven to eight week difference between peak breeding in the two habitats (Fig. 13.3; see, also, Chap. 9).

Nesting Success

Nesting success may be measured in many ways (Table 13.1), but the information generally of most interest is the overall production of fledged young in relation to the number of eggs laid. The percentage of tody eggs yielding fledglings was 53.6% and the number of "entire" nests (i.e., nests with the number of eggs and young undetermined) yielding fledglings was 61.7%. This degree of success, while comparable to that of temperate and tropical hole-nesters and of temperate cup-nesters (e.g., Rough-winged Swallow, *Stelgidopteryx ruficollis*, 68%; Southern House Wren, 62%; Yellow Warbler, *Dendroica aestiva*, 54%), is considerably higher than found in the

TABLE 13.1

NESTING DATA FROM 1968-69 AND 1969-70 SEASONS, COMPARING *mexicanus* FROM RAINFOREST AND SCRUB

	LUQUILLO RAINFOREST	GUANICA SCRUB	TOTAL
No. holes measured	492	87	579
Ratio of holes attempted to holes used	3 : 1	1.6 : 1	2.6 : 1
No. of completed, used nests studied [1]	80	32	112
No. of nests yielding fledglings	40 (50%)	29 (91%)	69 (62%)
No. of above nests with precise data	44	11	55
a) No. eggs laid	105	18	123
b) Av clutch size	2.39	2.22	2.36
c) No. eggs hatching	77 (73.1%)	17 (94.4%)	94 (76.4%)
d) No. nestlings flying	53 (68.8%)	13 (76.5%)	66 (70.2%)
e) % flying from eggs laid	50.5%	72.2%	53.6%

1) In many if these nests I could not see exact numbers of eggs and/or nestlings, but was able to determine the fates of the entire nests.

tropical cup-nesters (e.g., Puerto Rican Emerald, *Chlorostilbon maugeus*, 27.6%) (data from Lunk, 1962; Ricklefs, 1969; and Kepler, MS).

Burrow Failures

Each year the ratio between the number of burrows started and the number of fledglings produced was high (Table 7.2; Fig. 13.4). Data from two seasons gave a 9.5 : 1 ratio in the rainforest and 6.7 : 1 ratio in xeric scrub (overall, 8.9 : 1).

The reasons for the abandonment of burrows were chiefly unsuitable soils, bank slippage from heavy rains, occupation by other vertebrates, and inadequate building techniques (Table 7.3). Most (97%) of all burrow abandonments occurred during excavation.

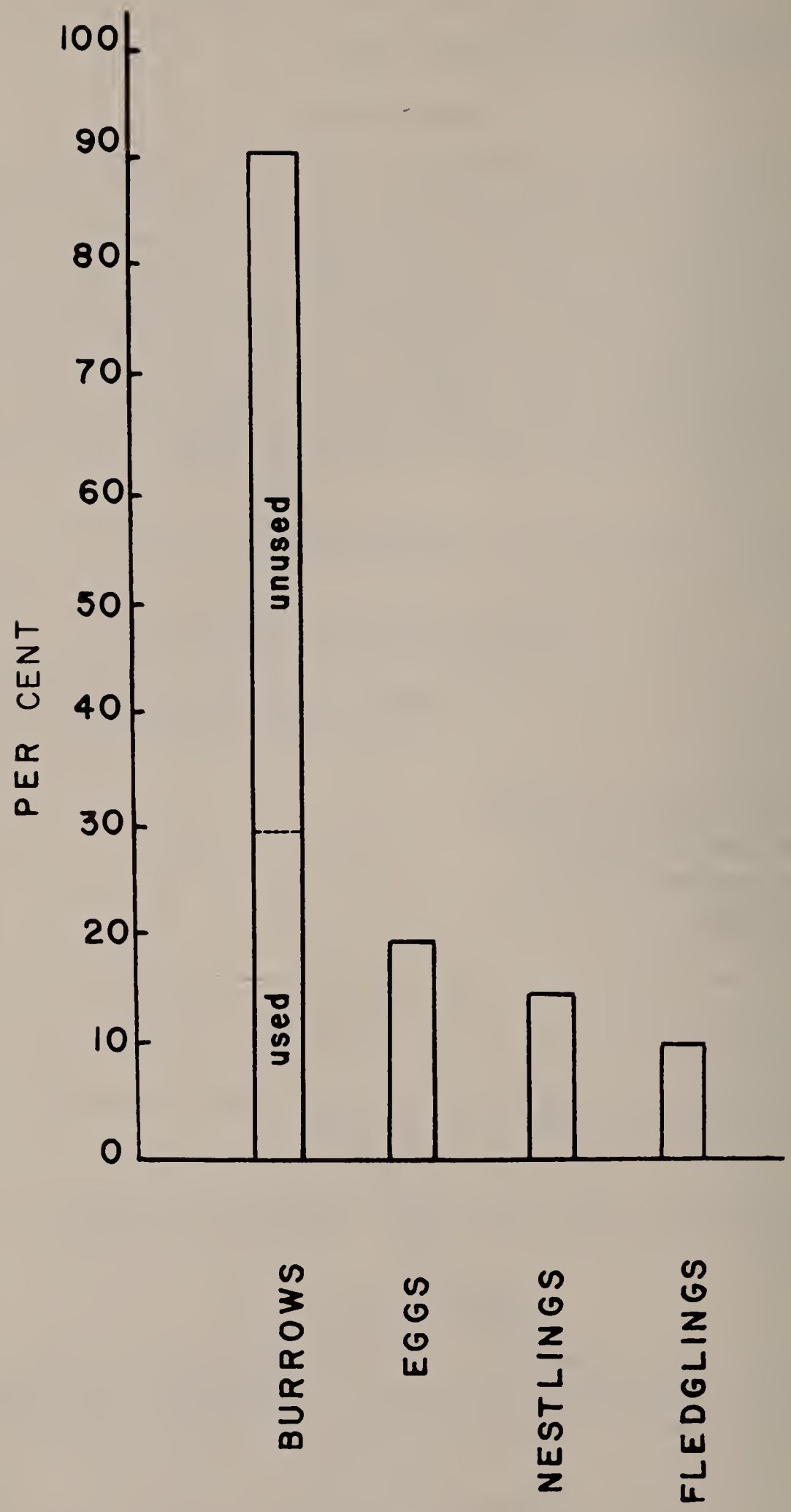


FIG. 13.4 Relative number of burrows, eggs, and nestlings to fledglings. Data from 492 fresh burrows, studied from 1968 to 1970.

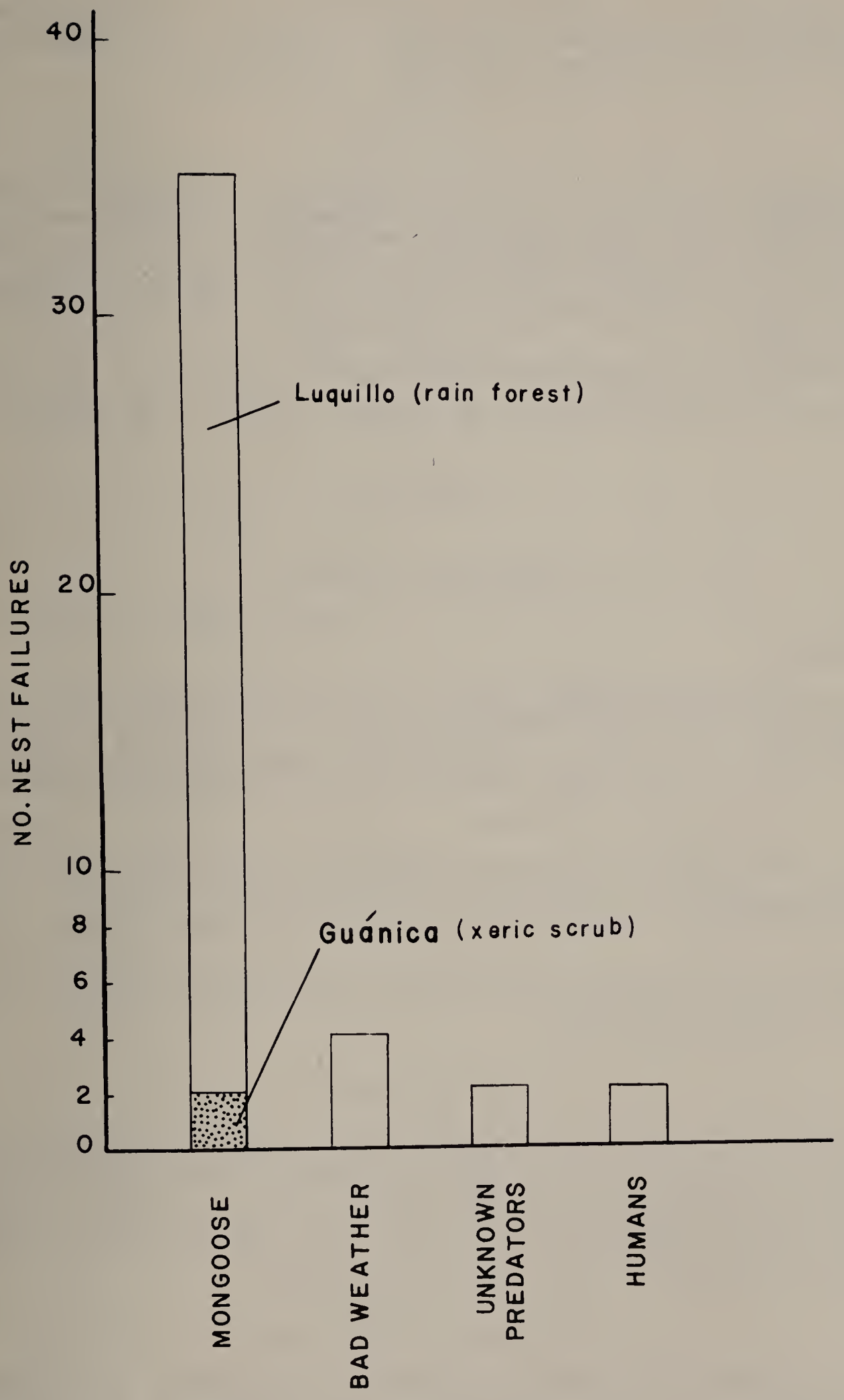


FIG. 13.5 Nest failures of *T. mexicanus* in rainforest and xeric scrub. Data are from 112 nests (80 and 32, respectively) from 1968 to 1970.

GENERAL ANALYSIS OF THE BREEDING SEASON

Nest failures can be attributed to mongooses, inclement weather, unknown small predators, and human interference, all resulting in the abandonment or destruction of the eggs or chicks (Fig. 13.5; Chap. 14).

Egg Losses

Egg loss in the rainforest was 27.6% (Table 13.2). Todies compare favorably with other hole-nesters (e.g., Rough-winged Swallow, 27.3%; Southern House Wren, 26%), all of whose egg losses are generally lower than those of birds with open nests (e.g., Puerto Rican Emerald, 37.3%; Song Sparrow, *Melospiza melodia*, 41.2%) (data from Lunk, 1962; Skutch, 1953; Kepler, MS; and Nice, 1937).

Although the sample was small, in the xeric scrub every egg studied is known to have hatched, with the possible exception of one infertile egg.

TABLE 13.2

BROOD LOSSES IN *T. mexicanus* [1)]

	1968 - 69	1969 - 70	TOTAL	
RAINFOREST				
No. nests with nestlings	22	46	68	
No. nests destroyed by mongooses	9	21	30	(44.1%)
XERIC SCRUB				
No. nests with nestlings	20	13	33	
No. nests destroyed by mongooses	2	0	2	(6.1%)
Total Brood Loss	11	21	32	(31.7%)

1) N = 101 nests

Therefore, total egg loss was at least five times greater in rainforest than in the scrub (27.6% to 5.6%).

Nestling Losses

Broods were lost in the rainforest seven times more frequently than in the scrub (Table 13.2). This is because mongooses, the sole cause of brood loss, are abundant in the former habitat but rare in the latter. Overall, three times as many broods were lost as were clutches (32 to 11), due primarily to mongoose destruction in the rainforest.

Altitude and Nest Success

The Tabonuco Zone, lowest in elevation, is undoubtedly the optimum habitat for todies in terms of vegetation, insect abundance, climate, soils, and the availability of nesting banks (Fig. 13.6; Chaps. 2 and 5; Kepler and Kepler, in prep.). This zone contained 57% of all the burrows found

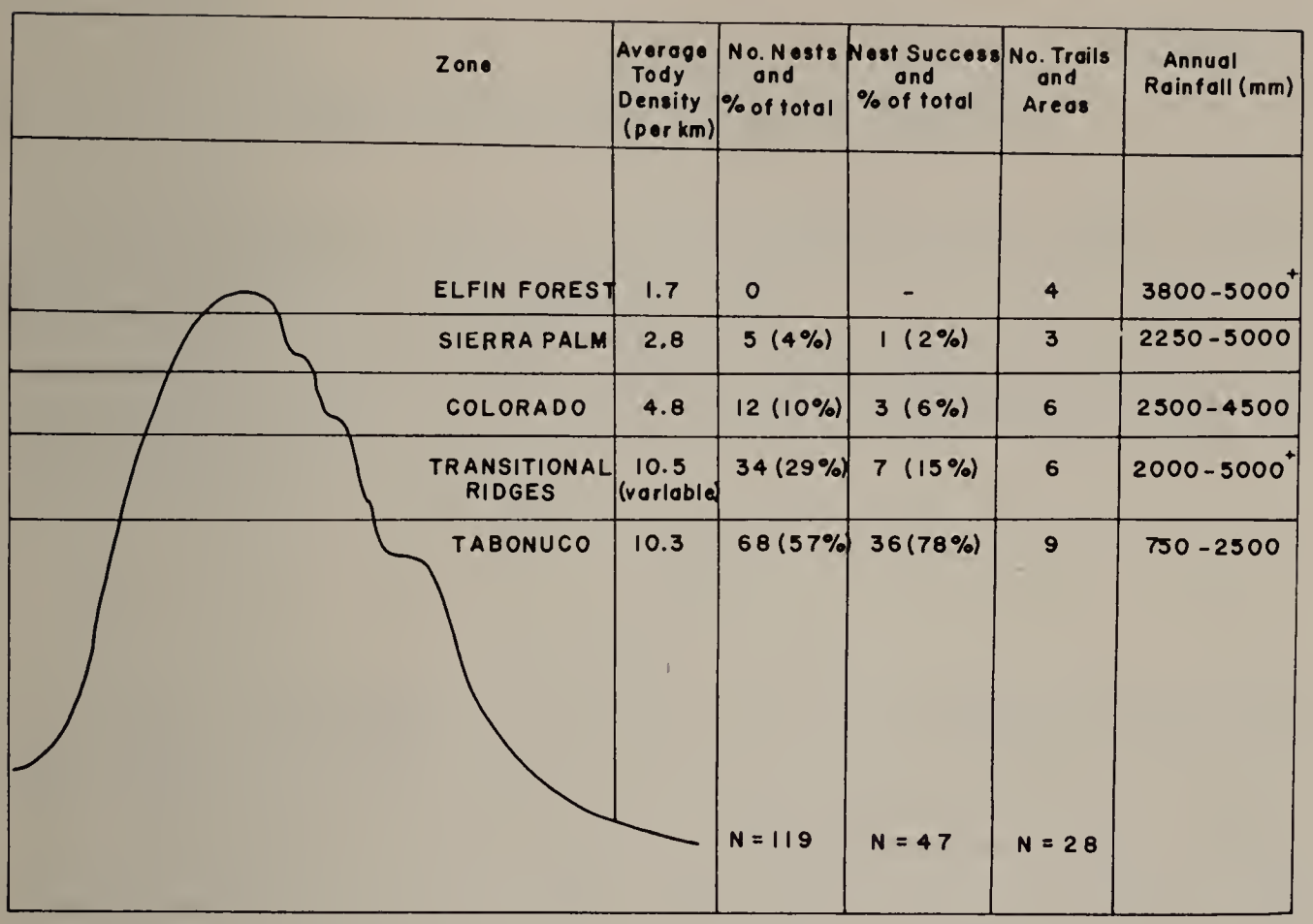


FIG. 13.6 Relation between elevation, linear tody density, numbers of completed burrows, and nest success in five vegetation zones of Luquillo Forest. Data taken from 1968 to 1970. Only burrows easily assigned to a vegetation zone were included; the names and localities of study areas are detailed in Appendix 2.

in the forest; 78% of all nest successes occurred here. The other zones, in descending order of productivity and ascending altitude, are the transitional ridges, Colorado Zone, Sierra Palm Zone, and, finally, with total failure, the Elfin forest.

14
POPULATION REGULATION

Detailed population studies of tropical birds are rare; the following discussion will shed some light on the factors that control population density in an insular species, the Puerto Rican Tody.

At least five regulatory factors appear to interrelate in a complex way. These are food, climate, predation, territoriality, availability of nesting sites, and interspecific competition.

Food

Methods of Study

In order to investigate the possibility of food limiting a population, one must measure for several years the abundance and availability of the chief items of prey and the quantity of each consumed, as well as assess the main causes of mortality and study the predator-prey interactions. Although these are virtually herculean tasks when dealing with insectivorous birds, a preliminary examination of these complex interactions was attempted through the following studies. (1) Monthly measurements were made of insect density at 10 stations (representing different vegetation zones or subhabitats) each in Luquillo and Guánica. By employing the simple technique of sticky flypaper (Chap. 1), we were able to measure the relative densities of insects, and seasonal variation, in each vegetation zone, as well as to document overall differences between the two regions. (2) A detailed study was made of the feeding behavior in rainforest, xeric scrub, and *cafetales*, yielding information concerning the location of prey within microhabitats, the quantities of food eaten by adults and young, and the types of food consumed from hatching to maturity. (3) A complete ecological study of birds in scrub and rainforest helped to identify possible avian competitors. Observations of frogs and anoles, aided by Drewry and Lavigne (unpub.) and Rand (1964) provided insight into possible competition from some nonavian vertebrates. (4) Daily measurements of weather were made at La Mina Field Station and supplemented data from other locations in Luquillo Forest and elsewhere in Puerto Rico (U.S. Weather Bureau; Weaver, pers. comm.). These data provided information on the direct effects of rain on feeding rates of adults and young, as well as on the frequency of bank slippages. (5) Early morning strip-censusing (Chap. 2) provided information on the relative abundance of both migrant and other resident birds, although we concentrated on the latter species.

Amount Consumed

In El Verde forest, one breeding pair of todies and their young consume approximately 1.8 million insects on a 0.7 ha plot during 5.5 months, the

average period when todies vigorously defend breeding territories. This calculation is based on data on the feeding rates of adults, on the rates at which the young are fed, on the average number of nestlings and fledglings produced, on the average size of the breeding territory, and on the estimated (Lavigne, unpub.) production of insects. Despite the substantial density of insects at El Verde (40^{12}/0.7 ha/5.5 months)., the proportion of the insect population available to todies is impossible to calculate. It is difficult, nevertheless, to conceive of todies encountering a limit to the availability of insects when such enormous numbers are present. However, not all of these vast numbers of insects are available, owing to their size or habitat, and the weather. It should be borne in mind that even though todies may take insects up to 40 mm long, they primarily capture small prey, that three-fourths of the tody's time is spent between the ground and half way up to the canopy, that more than three-fourths of the tody's food is captured from the underside of leaves, and that todies never feed in the ground litter (Chap. 6), all factors that restrict the availability of prey. Furthermore, there is evidence that during torrential rain todies have difficulty in finding sufficient food for nestlings, because the insects hide or are washed from leaves. The effect of the rainy season is compounded by the fact that the birds are breeding then and hence their foraging area is more restricted than in the nonbreeding season.

Evidence for Influence on Population

Relationship between Tody and Insect Densities

One finds variable densities of todies, depending on habitat, elevation, vegetation zone, canopy height, abundance of insects, and the presence of streams and nesting banks (Chaps. 2, 4, 13). Within the rainforest the densest populations occur in lower montane zones (especially if partly disturbed), where the insect density is highest; both tody and insect populations then decrease with higher elevation (Fig. 13.6; Kepler and Kepler, in prep.).

In Luquillo a pronounced peak in insect production occurs from April to June; this is also when the numbers of burrows with nestlings is at its peak (Fig. 14.1).

The conclusion that there is a positive correlation between insect and tody populations seems irrefutable.

Nest Helpers

Supernumerary adults are not obligatory for the success of a nest, but in Luquillo roughly half of the studied nests had three or four adults, chiefly helping to feed nestlings (Chap. 12). These nests contained significantly larger average clutches and had greater nesting success than those nests without helpers. Nest helpers appear to represent an adaptation to ensure survival of young during adverse weather when foraging is difficult. This,

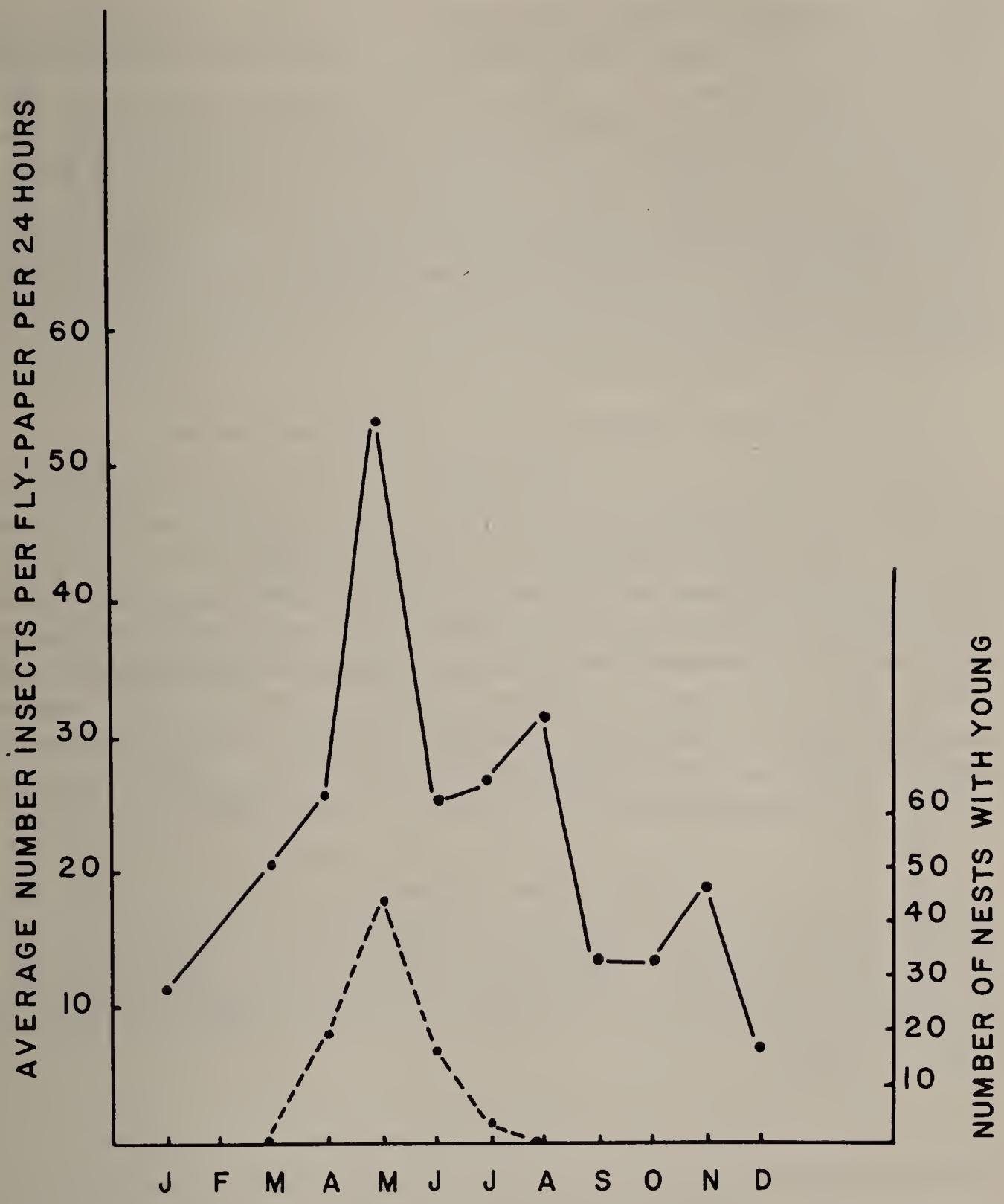


FIG. 14.1 Relationship between insect densities and numbers of nestlings in rainforest, by month. Data derived from 120 flypapers, 10 sites from 200 to 1000 m in elevation, and 2,510 insects, measured between December 1970 and November 1971.

in turn, again emphasizes the relationship between food and population size.

Brood Size

Adult todies capture enormous amounts of food, averaging one to two insect captures each minute from dawn till dusk (Chap. 6). The nestlings

also consume insects at some of the highest rates recorded for insectivorous birds (Chap. 10). I believe that brood size is limited by the *time* available to feed nestlings, hence two or three chicks probably represent the limit that adults are physically capable of feeding, while still nourishing themselves. As insect density is higher in scrub than in wet forest (Kepler and Kepler, in prep.) and todies feed faster in the former (1.8 and 0.8 insects/min, respectively), it is possible that scrub todies can raise more young. Limited data on fledglings surviving at least one day indicate that each scrubland pair raised an average of 1.11 juveniles (N = 28) compared to only 0.88 in the rainforest (N = 8).

Character Displacement in Hispaniolan Species

T. subulatus and *T. angustirostris* are examples of Gause's Principle that two related and ecologically similar species cannot coexist (Chap. 2). When these two species are sympatric their feeding strategies differ markedly. In fact, their differences are greater than those between any of the other species of *Todus*. When the taxa are sympatric, the Broad-billed feeds higher in the canopy, sits for longer periods between flights, and flies longer distances from its perch than when it is allopatric, while the Narrow-billed behaves contrarily (Fig. 6.4; Table 15.2). Associated with this, their bill widths and lengths diverge from other todies (Tables 1.2, 15.1). These differences again stress the importance of food as the mechanism regulating tody populations.

Interspecific Competition

No other bird, or other vertebrate, in Puerto Rico obtains even as little as half of its food from the same source as does the tody. But, nevertheless, interspecific competition for food may be of some importance in scrub forest (see Chap. 6).

Climate

Climatic conditions such as torrential rains, prolonged inclement weather, fog, and temperature affect tody populations, both negatively and positively, as well as directly and indirectly (Chaps. 7 and 9). These factors relate almost exclusively to wet, forested habitats.

Landslides destroyed or caused todies to abandon 12% of newly begun burrows and 7% of their clutches (Table 7.3). Although suitable nesting banks and potential burrows may be destroyed by heavy rain, rain also plays an important role in creating new banks. We know that todies center their territories around suitable banks, attempt several holes before completing a useable one, and are more successful breeders in moderately-vegetated soils than in bare or well-vegetated surfaces (Table 7.3). The availability of suitable nesting banks thus depends on slippages every few years to provide a continuous supply of moderately-covered surfaces within the birds' limited home-ranges.

POPULATION REGULATION

In high elevation elfin forest, where fog is almost continuous and soils are perpetually waterlogged, the climate creates unfavorable nesting conditions.

Two chicks starved during an exceptionally wet week in Luquillo, when at least three adults were unable to feed them (Chaps. 10 and 12). I found two other nests invaded by stinging ants, and suspect that the ants were attracted to decaying nestlings that had starved during torrential rains. Other chicks, none of which survived, appeared to have been forced from these nests prematurely by the ants. Thus, the temporary decrease in food supply during adverse weather may directly affect nesting success, as in the first example, and possibly does so indirectly, as in the second.

PREDATION

MONGOOSE (*HERPESTES MUNGO*, MUSTELIDAE)

Indian Mongooses, the major predatory threat to todies, account for 81% of nest failures in the rainforest and 6% of the failures in xeric scrub. The animal is rare in the latter region, probably because of lack of fresh water.

Introduced into Puerto Rico in 1877 to control rats, these aggressive pests now range over the whole island, carrying rabies, killing domestic chickens and surviving in remote areas mostly on lizards, frogs, centipedes, spiders, a variety of insects, and, rarely, rats (Wadsworth, 1949; Wolcott, 1953). Mongooses destroy most tody burrows when there are young in the nestling stage. They presumably are attracted by the foul odors emanating from them. They claw into the small tunnels, enlarging them until the chamber is reached. As all the destroyed holes were of approximately the same diameter (av. 11 cm wide and 10 cm high) and appeared similar to the one I knew for certain had been entered by a mongoose, I believe the possibility of rat predation may be eliminated. Rats have much smaller body girths and are nocturnal; if they were responsible one would expect that brooding or attending adults would have been taken too, which they were not, as todies are reluctant to leave the nest at night.

There is a definite correlation between the height at which todies build their nests and the incidence of their destruction (Fig. 14.2). In the rainforest, 59% (N = 27) of all nests below 0.8 m were destroyed by mongooses (av. height 0.4 m). It appears that 0.8 m is an approximate critical height above which the mongoose either cannot smell the chicks' excreta or cannot climb the vertical slope. In every case where a burrow was destroyed above this height the mongoose had climbed from above or the side.

Since todies build their burrows at an average height of 0.9 m in Luquillo and at half this height in Guánica, it is probable that the Puerto Rican Tody is undergoing a gradual evolution toward placing its nests higher in the rainforest than in the coastal scrub.

Attewell (1907) mentions predation by mongooses on Jamaican todies;

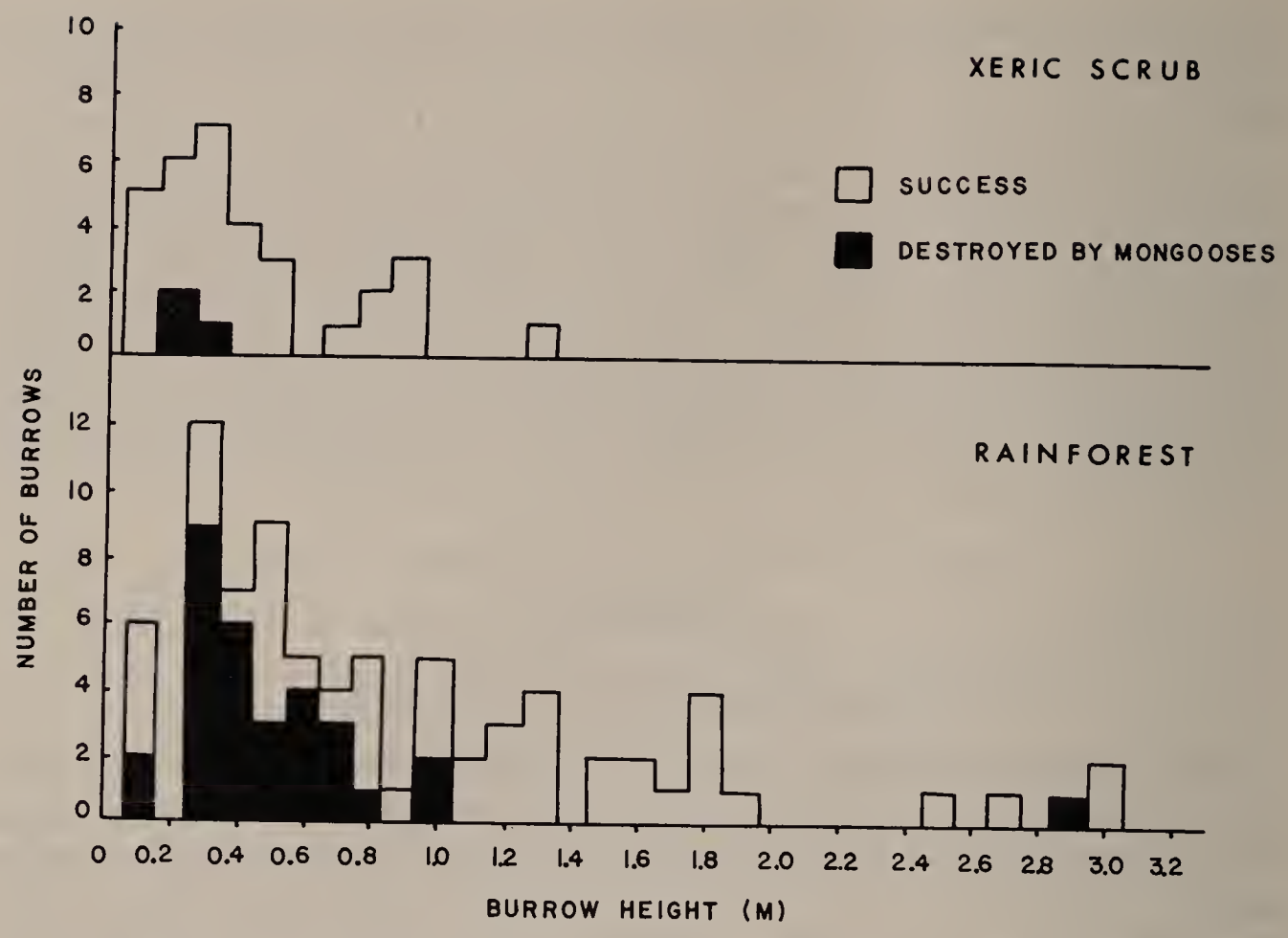

XERIC SCRUB
SUCCESS
DESTROYED BY MONGOOSES
RAINFOREST
NUMBER OF BURROWS
BURROW HEIGHT (M)
0 0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8 2.0 2.2 2.4 2.6 2.8 3.0 3.2

FIG. 14.2 Relationship between burrow height and mongoose predation in rainforest and xeric scrub.

I saw burrows that had been destroyed by mongooses in both Jamaica and Hispaniola.

BIRDS

The Pearly-eyed Thrasher (*Margarops fuscatus*), an aggressive mimid, occuring in densities up to 27 pairs/ha in Luquillo Forest, devours fledgling, and possibly adult, todies. Whenever thrashers are close to juvenile todies the adults chase them energetically, vocalizing rapidly and Wing-rattling.

Barn Owls (*Tyto alba*), which are common in some regions of the Dominican Republic, apparently capture occasional todies. Wetmore found a skull of *T. angustirostris* in a Barn Owl cave (1927), and Olson (pers. comm.) recently unearthed three humeri of *T. mexicanus* from a cave in Puerto Rico, dated at approximately 17,000 years. Curiously, these bones are smaller and more slender than those of present-day populations. As todies roost high in trees it is possible that any owl may take a few todies. Olson (1976) feels certain that *Paleotodus emryi,* the recently discovered fossil from Wyoming, had been consumed by owls.

A possible predator is the Sharp-shinned Hawk (*Accipiter striatus*). On six occasions, either I or my husband saw this raptor with small birds in its talons, some of which may have been todies.

The Red-tailed Hawk (*Buteo jamaicensis*) is common in Luquillo; todies

generally halt vocalizations and move farther into the underbrush when these hawks scream overhead.

Humans

Today Puerto Rico is sufficiently prosperous so that todies are not unduly bothered by children seeking supplementary protein. However, in rural areas elsewhere in the Greater Antilles, where people live at subsistence level, children dig out tody holes to take eggs and trap adults, and eagerly kill adults with slingshots. As todies concentrate along roads and trails, they are most susceptible to this type of predation. For example, in a steep six-hour climb in Hispaniola I found 20 old, dug-out *T. subulatus* holes and none that had been unmolested. Wetmore and Swales (1931) also mention this problem in Hispaniola.

Miscellaneous Predators

Potential and actual predators that I found occupying old burrows included snakes, lizards, treefrogs, stinging ants, whipscorpions, and burrowing snake-like lizards. Five nests lost 12 eggs without the obvious enlargement of their entrances as typical of mongoose predation; any combination of the above animals may have been responsible. Stinging ants probably hastened the exit of two broods and a snake devoured one brood.

Territoriality

Xeric Scrub

Nesting banks are much scarcer in scrub than in rainforest, territories are smaller, and aggressive behavior is more marked throughout the year (Chaps. 2, 4, and 7). The number of burrows attempted in 1970 that were within 3 m of those begun in 1969 was 28 times greater in Guánica than in Luquillo. Since each tody pair defends a nesting bank, and banks are limited, it follows that territorial behavior is probably important in controlling the population size of todies. Pairs of any species of tody living in lowland marginal scrubby areas will attempt to breed in unsuitable banks, such as levelled crumbly earth, sand patches, rocky soils, or even in low drainage ditches in sisal fields. Obviously, they must be forced to these sites by a shortage of proper banks.

The two forested areas I visited in Jamaica have high insect densities (they support six species of flycatchers), but todies are uncommon (Table 2.2). This is doubtless because the forest virtually grows out of limestone bedrock, which provides few banks suitable for todies.

Rainforest

Here, where nesting banks are more common and continually replenished, tody territories are often widely-spaced and are defended vigorously only

in the breeding months. Territorial behavior seems less important in population control here than in dry regions.

Interspecific Competition

Interspecific competition seems to play a small role in regulating tody populations. There is no avian competition for nesting banks, as there are no other bank-nesting birds in the Caribbean. Puerto Rican Todies abandon fresh burrows occupied by anoles or treefrogs; other burrow visitors such as whipscorpions and "tarantulas" could conceivably cause similar behavior, but none of these animals can be considered to be a significant competitor.

Interspecific competition for food is a factor chiefly relevant to scrub forests. It is discussed fully in Chapter 6.

Relative Importance of Regulatory Factors in Rainforest and Scrub

A differently weighted combination of factors appears to control tody populations in scrub and rainforest. These data, although derived from the Puerto Rican Tody, probably can be generalized to include other *Todus* species. I propose that in the rainforest the major factors, in order of their importance, are: (1) predation, principally during egg, nestling, and fledgling stages; and (2) food supply, especially during the breeding months, when it is profoundly influenced by climate.

In xeric scrub, the chief factors are probably: (1) territoriality and the related availability of nesting banks; and (2) food supply, influenced by interspecific competition, especially during the breeding season.

Hence, we find a mixture of density-dependent, density-independent, and behavioral factors at work, interrelating in each habitat to maintain a relatively constant population size.

15
SIMILARITIES, DIFFERENCES, AND EVOLUTION WITHIN THE FAMILY

The family Todidae is small and well-defined. Its five species are very similar morphologically and, as far as is known, are also very alike in behavior and ecology. The similarities and differences within the family which have been detailed in earlier chapters are here briefly summarized and tabularized (Table 15.1). The presumed evolutionary history of the family is also outlined.

Characters Shared by all Species

The list below of shared characters is far from complete. I observed many instances of behavior in one or two species that may or may not be typical of the whole family. For example, it is not known if all five species have nest helpers, or if the courtship patterns observed in *T. mexicanus* are the same throughout the family, or if the Hopping Display seen in *T. angustirostris*, the function of which is unknown, also occurs in other species.

Morphological Similarity

The five species of todies generally closely resemble each other in size, color, and plumage pattern. Differences in flank, iris, and undertail covert coloration, plus small variations and differences in the pattern and distribution of color in other areas, differentiate the species in adult plumage, although the immatures are markedly alike, lacking the colorful patches of adults.

Ecological Tolerance

All species inhabit xeric scrub, rainforest, *cafetales*, second-growth, and the margins of mangroves. Population densities are greatest in limestone forests and *cafetales*, except for *T. angustirostris* which favors lush, high elevation pine or rainforest. Insect abundance, predators, climate, type and availability of nesting banks, and inter- and intraspecific competition are all factors appearing to limit population densities and to determine the habitat preference of the five species.

Feeding Behavior

All species capture prey from a variety of substrates, principally by leaf-feeding (flying in an arc to the underside of leaves) but also by Air-feeding and other less-used methods. As far as our limited data will permit comparison, their insectivorous diets are similar, being chiefly small flies, beetles, and lanternflies, supplemented by crickets, grasshoppers, cockroaches, moths, caterpillars, spiders, and other insects.

TABLE 15.1

COMPARISONS OF FIVE *Todus* SPECIES [1)]

	multicolor	*subulatus*	*angustirostris*	*todus*	*mexicanus*
No. specimens (322)	82	83	26	27	104
MORPHOLOGY					
Av bill length (mm from distal nasal orifice)	12.3	14.3	12.6	13.9	13.3
Av bill width (mm at distal nasal orifice)	4.3	5.4	3.9	4.4	4.4
Av wing chord (mm)	43.8	50.3	46.0	46.0	42.8
Av tarsus (mm)	12.8 (N=13)	14.0 (N=25)	12.8 (N=12)	11.9 (N=12)	11.7 (N=16)
Av weight (g)	-	-	-	6.4 (N=12)	5.4 (N=3)
Iris color	females slate, males white	most slate	most white	random white & slate	females white, males slate
Av amount of visible pink on flanks [2)] (and/or breast & belly)	2.1	2.9	1.0	0.5	some vestiges in 3 male skins
Yellow undertail coverts	small patch	small, some on belly	small patch	yellow-green, extends over belly & breast	bright, extends to flanks & lower belly
Yellow-green, almost iridescent eyebrow	conspicuous	conspicuous	partly	none	none
Yellow-orange forehead lores	none	none	conspicuous	none	present
Cheek - patch (subauriculars)	distinct, bright sky-blue	few gray feathers	few gray feathers	blue-gray indistinct, especially in females	few gray feathers
Av amount of blue on wrists [3)]	present - 1.4	almost absent	faint - 0.3	absent	present - males 1.9 females 1.2
Blue on secondaries and tail	little	none	none	none	trace
Gray breast, especially sides and when freshly molted	yes	very pale	yes	pale	yes
Green on breast	none	none	none	distinct, a continuous band at times	pale in immatures
EGGS					
Av length X width	15.5 X 12.6 (N=5)	16.9 X 14.3 (N=36)	15.5 X 13.5 (N=5)	16.1 X 13.3 (N=28)	16.5 X 13.5 (N=15)

TABLE 15.1 (CONTINUED)

BEHAVIOR					
Flank Display	probably striking, greatest height not seen	most striking	striking	least striking	virtually absent
Wing-flicking	occasionally	constant, pulls wings up highest	constant	often, not constantly	sometimes, barely perceptible
Bobbing	frequent, not as much as *mexicanus*	none	none	none	frequent, especially when aggressive
Hopping Display [3]	?	?	yes	?	no
Characteristic Vocalization	lively,4-parted whistle	single,clear,rather metallic note,repeated monotonously	double, buzzy note, "Chip Chui"	single, nasal Beep like *mexicanus*	single nasal Beep

1) Data from 322 specimens from U.S.N.M., Carnegie Museum and Royal Ontario Museum
2) See Table 5.2 for explanation of 0 to 5 scale
3) Scale 0 to 3

SIMILARITIES, DIFFERENCES, AND EVOLUTION

All todies forage well below the forest canopy. In all but *T. subulatus* 50% of all flights seen are below four-tenths of the canopy's height and 90% are below nine-tenths canopy height, regardless of the habitat. *T. subulatus* forages higher, especially when sympatric with *T. angustirostris.* Todies feed lower in xeric scrubland (av 2.3 m) than in rainforest (av 4.2 m).

The five species forage with similar efficiency, despite differences in activity. In dry scrub each species captures more insects per minute, and for any given number of flights, than in rainforest (41% to 33% efficiency, respectively).

Rapid Metabolism

Each species feeds from dawn to dusk (up to 14 hr), consuming enormous quantities of food, and averaging 1.7 feedings/min in xeric scrub and 1.0 feeding/min in rainforest. Undoubtedly all tody chicks have metabolisms as rapid as that of *T. mexicanus,* in which species each nestling consumes up to 140 insects per day, one of the highest rates known for small insectivorous birds.

Agonistic Behavior

Wing-rattling, accompanied by Chasing and supplanting attacks is the basic element of territorial behavior among all species, although it is supplemented by Throat-rattling in *T. todus.* I observed Crest-raising, Fluffing, Wing-flicking, and Flank Displays in all species; elements of rarer behavior are undoubtedly also shared.

The amount of pink flank feathering appears to be directly correlated with the intensity of flank displays. It is most intense in *T. subulatus* and least intense in *T. mexicanus.*

Reproductive Behavior

Todies are nonsocial, solitary nesters which remain paired throughout the year. Increased territoriality is evident during the nesting season in the spring and summer.

All todies build burrows of a similar size and shape (av 3.7 mm wide, 3.9 mm high, 30.0 mm long), and prefer shaded vertical banks with workable soil. They excavate fairly close to the ground (av 1.4 m; lowest in xeric scrub) in banks which average less than 2 m high. Many burrows are begun before one is completed.

The eggs are thin-shelled and their average size is 16.0 × 13.4 mm. In *T. mexicanus* the mean weight of the egg is 1.43 g, which is 26% of the bird's body weight. It is a relatively large egg for a bird of this size. The incubation period is long but whether this accounts for the large egg, or vice versa, is unknown.

Clutches generally consist of two to three eggs. All evidence indicates that there is only a single brood each year.

SIMILARITIES, DIFFERENCES, AND EVOLUTION

Maintenance Activities

All species Rain-bathe, Bill-wipe, Regurgitate, Fluff, Shake, Preen, and Head-scratch similarly. No differences have been noted.

Vocalizations

Todies produce simple, unmusical whistles or buzzy, nasal sounds, and even though the characteristic vocalizations of each species are distinctive, each possesses sounds in its repertoire which link it to others, as detailed in Table 3.1 and below.

Evolution of the Family

Fossils and Derivation from Primitive Motmot Stock

I have detailed (Chaps. 1, 10) many morphological, behavioral, and developmental characters demonstrating that todies are more closely related to motmots than to kingfishers, although this evidence contradicts the conclusions of Sibley and Ahlquist which are based on an analysis of egg-white proteins. In addition, recent paleontological discoveries, including an analysis of the biogeography of fossil alcedines, show that the Todidae were derived from a motmot-like ancestor in the Oligocene or earlier (Olson, 1976). The Todidae probably were once widespread in North America, and therefore the present range of the family is relictual. *Palaeotodus emryi* (Oligocene of Wyoming) is the only tody known earlier than the late Pleistocene remains of modern-day species, and is most closely related to the Tody Motmot (*Hylomanes momotula*), the most primitive genus of the Momotidae. This agrees with osteological studies of *Todus* (Murie, 1872ab; Sclater, 1872ab). Unfortunately, no behavioral comparisons are possible between todies and tody motmots, as the latter is little known in life. It is a solitary bird of undergrowth in humid tropical and subtropical forests, feeding by sitting motionless for long periods, then rapidly darting out to capture prey in a manner similar to puffbirds and some other motmots (Meyer de Schauensee, 1964: 168; Slud, 1964: 173). We have further noted (Chap. 10) that in its small size, short tail, pterylosis, and physical appearance, it resembles nestlings of the larger motmots and adult todies. *P. emryi* was larger than *Todus* (its fragmentary remains suggesting a size close to *Hylomanes*) with a proportionately shorter and thicker bill and larger wings, thus possessing greater powers of flight.

In the light of this new fossil, and another one indicating an Old World origin for motmots, Olson suggests that the motmot–tody group may have been entirely supplanted in Europe, then drastically restricted in North America with the deterioration of tropical conditions in the late Tertiary. Thus motmots became confined to Central America after spreading southward, and todies were similarly restricted to an unknown neotropical area, finally resulting in isolated West Indian relicts. Two possibilities thus arise: (a) a primitive tody-ancestor was widespread in North America and the

FIG. 15.1 Probable evolutionary pathways in the Todidae. Dotted lines indicate depth of 200 m, which would have been dry land at peak of the last glaciation.

West Indies, leaving only a few island populations which differentiated in isolation in the Greater Antilles; or (b) a primitive tody ancestor colonized the West Indies from Central America, thence speciating linearly and eastward in more recent times. I favor this latter viewpoint, considering the morphological uniformity of the Todidae, the large size and strong wings of *P. emryi*, and other factors considered below.

Therefore, todies probably arose from a short-billed Central American prototype resembling either *Palaeotodus* or *Hylomanes*. The West Indies, true oceanic islands (i.e., they have never been connected to the mainland), were colonized by birds via four routes: the Yucatán Peninsula to Cuba, Florida to Cuba, the Nicaraguan bulge to Jamaica, and Venezuela to Trinidad and the Lesser Antilles. This *Palaeotodus*-like ancestor (or "Protodus") appears to have followed the Yucatan pathway, a relatively short distance, shrinking to less than 150 km during the last glaciation, as indicated in Figure 5.1. Bond (1948, 1966) points out that Caribbean bird dispersal is due mainly to hurricanes, as the prevailing easterly trades have had little effect on its avifauna. One needs only to consider the west-east passage of migrant warblers and shorebirds, and the expansion of white-eyed parrots (*Amazona* spp.), trogons, pigeons, and vireos throughout the Greater Antilles, to verify the possibility of bird distribution against the prevailing winds. Also, Lack (1976) has demonstrated in painstaking detail that most Jamaican land birds were derived from Honduras, and that the present avifauna of that island

is more closely allied to that of Central America than to that of elsewhere.

The five species of todies fall into two seemingly natural groups, viz., the Cuban, Broad-billed, and Narrow-billed (*multicolor, subulatus* and *angustirostris*) species and the Jamaican and Puerto Rican (*todus* and *mexicanus*) species. These groupings appear to have had their origins in the evolutionary history of the genus.

I propose that the Cuban Tody (*multicolor*) expanded to Hispaniola where it differentiated into the (ancestral) Broad-billed (*subulatus*) bird, which in turn became split into two isolated populations and differentiated into the Broad-billed and Narrow-billed Todies (*angustirostris*) as now known (see details in Chap. 2).

The Jamaican Tody (*todus*) seems to have been derived from Cuba and the Puerto Rican species (*mexicanus*) from Jamaica (Fig. 15.1). The latter route seems unlikely owing to the direction of the prevailing wind and to the closeness of Hispaniola and Puerto Rico; one would expect colonization to have been across this small gap. There are a few species of birds that are (or were) restricted to Hispaniola and Puerto Rico (for example, White-necked Crow, *Corvus leucognaphalus;* Antillean Mango, *Anthracothorax dominicus;* Hispaniolan Parakeet, *Aratinga chloroptera*). On the other hand, there are no species restricted to Jamaica and Puerto Rico, although the newly-discovered Elfin Woods Warbler (*Dendroica angelae*) of Puerto Rico is closely related to the Arrowheaded Warbler (*Dendroica pharetra*) of Jamaica (Kepler and Parkes, 1972), a situation parallel to the *todus-mexicanus* relationship I postulate.

Let us now examine the evidence in favor of these proposed evolutionary pathways, and against alternate ones, drawing on material from Table 15.1:

MULTICOLOR→ ANCESTRAL *ANGUSTIROSTRIS*

Both Hispaniolan species are relatively specialized. Therefore, it is not possible to postulate a direct Cuban to Broad-billed to Narrow-billed Tody evolutionary pathway (see below). The following characters indicate the closeness of the Cuban to the Broad-billed Tody rather than to the Narrow-billed Tody. Either a single or double invasion could have accounted for the presence of a Broad-billed Tody ancestor on Hispaniola.

Plumage.—The brilliant, shining green plumage of *multicolor*, shot with yellows and blues, forming a pale, wide, motmot-like, almost iridescent eyestripe, is similar to that in *subulatus*. Other species have darker green plumage with no eyestripe (faint in *angustirostris*). Both *multicolor* and *subulatus* have small white "mandibular beards," and their red gorget feathers are more tipped with white than in other todies. *T. multicolor* and *subulatus* have the greatest amount of visible pink on the flanks, with it spreading over their breasts and bellies, other species have considerably less or none.

Flank Displays, accompanied by rapid, exaggerated Wing–flicking, are more pronounced in *subulatus* and, I predict, in *multicolor*, although as I did not observe the latter tody during the breeding season, I was not able to see the height of its display.

SIMILARITIES, DIFFERENCES, AND EVOLUTION

Behavior.—Subjectively, *T. multicolor* and *T. subulatus* behave and appear very similar. They stand higher and lean forward, stretching their necks more than other todies; they also sit less upright, appearing sleeker, less puffed-out and more streamlined. They are the least active of the group, sitting for relatively long periods between flights.

Vocalizations.—Although *T. multicolor* characteristically whistles a lively four- or five-part call and *T. subulatus* a single, clear note, repeated monotonously, the vocal *qualities* of each are alike. Notes of other species are more nasal and buzzy, for which the words "clear" and "whistle" are inappropriate.

Ancestral *subulatus*→ *subulatus* and *angustirostris*

The two Hispaniolan species, which are similar morphologically, are the most specialized in behavior of the Todidae (Chap. 2).

I believe that the ancestor of the two Hispaniolan species most closely resembled *T. subulatus*, because, first, *T. subulatus* is a more generalized species, with a wider ecological tolerance, adapting best to xeric scrub but ranging (sometimes in large numbers) from lowland mangroves up to high elevation rainforest and pines. *T. angustirostris*, on the other hand, is generally restricted to lush, high elevation forest, although it occurs in small numbers in other habitats; even at lower elevations it seeks moist ravines. Many morphological and behavioral characters present in *subulatus* are less obvious or absent in *angustirostris*. These are, for example, the light iridescent eyestripe, the degree of pink flank coloration, the white "mandibular beard," the pale shining plumage, its less active habits, and its more horizontal stance.

Specialization of each species.—The Broad-billed Tody, even though euryoecious, is basically desert-adapted. In general, animals living in deserts are larger, paler, and have longer appendages than those inhabiting humid regions (Bergmann's, Gloger's and Allen's "rules"). Thus, *subulatus* exhibits the longest wing, tarsus, and bill and the widest bill of all five species; the palest coloration in the family, especially in the red of the gorget and gray of the breast; the sleekest, most streamlined appearance; and the ability to fly farthest.

On the other hand, *angustirostris*, essentially a moist forest bird, has the darkest plumage, including much gray on the breast, of any species, a black tip on the mandible, which sometimes extends almost to its base; the narrowest and second shortest bill (next to *multicolor*) in the family. Its wings are shorter than those of *subulatus*, but not so much as one would expect from its small flights and skulking habits.

Character displacement.—There is no doubt that *subulatus* and *angustirostris* have diverged from other forms of *Todus*, both in morphology and behavior. In addition they show striking behavioral divergences between themselves because of their sympatry.

Differences from other species.—Their bill lengths and widths, wing lengths, and egg dimensions differ more between one another than between any

TABLE 15.2

MORPHOLOGICAL AND BEHAVIORAL DIVERGENCE OF THE TWO HISPANIOLAN SPECIES FROM "TYPICAL" TODIES

CHARACTER	*angustirostris*	other spp.	*subulatus*
Average bill length (mm)	12.6	13.2	14.3
Average bill width (mm)	3.9	4.4	5.4
Average wing length (mm)	46.0	44.1	50.3
Average egg length X width (mm)	15.5 X 13.5	16.0 X 13.1	16.9 X 14.3
Average foraging height in rainforest (m)	2.3 (sympatry)	4.8	5.2 (sympatry)
Average foraging height in scrub (m)	1.7	2.5	6.5
Average flight length (m)	0.8 (sympatry)	1.4	2.3 (sympatry)
Maximum flight length (m)	7 (sympatry)	17	40 (sympatry)
Average sitting period while foraging in rain and scrub forests (secs)	5.3	10.5	30
Average no. flights per min in rainforest and scrub	8.0 (sympatry)	4.4	2.0 (sympatry)

other combination of the five species (Tables 15.1 and 15.2).

In *subulatus* and *angustirostris* there appears to have been selection for iris color, resulting in *subulatus* having mostly slate and *angustirostris* mostly whitish irises, in contrast to more general occurence of both colors in each of the other species (Table 15.1).

The foraging behavior of these two species also diverges from that of "typical" todies, as illustrated by flight distances (average and maximum), number of flights per minute, length of sitting periods, and foraging heights (actual and relative to canopy height; see Table 15.2).

Reproductive isolating mechanisms in subulatus *and* angustirostris.—Although superficially alike, as many as five differences are found between these two species: (1) The Narrow-billed Tody has a black-tipped mandible, darker plumage, and normally has less pink exposed on its flanks; it rarely Air-feeds but sometimes gleans like warblers; it generally sits hunched close to its perch. All these characters are not present in the Broad-billed Tody. Limited observations indicate that *angustirostris* might have more elaborate courtship displays (for example, Hopping display, Chap.5). (2) Their typical vocalizations are single and double calls, respectively, but their chattering alarm calls are similar, although heard much more often in *angustirostris.* (3) Observations on the number of Wing-rattlings and number of fresh nests found in April and May indicate that *subulatus* breeds earlier in the season than does *angustirostris.* (4) Differences in feeding behavior are striking and have been fully discussed (Chap. 6); briefly, *subulatus* forages higher and

less actively than does *angustirostris*, it flies farther, and it sits longer between forays, therefore, flying fewer times each minute; these differences are accentuated when the two are sympatric (Table 6.1; Fig. 6.4). (5) The two species are generally separated by habitat and elevation; however, *angustirostris* is not so confined to dripping rainforest as was previously thought (Wetmore and Swales, 1931; Bond, 1971) and *subulatus* is not exclusively a lowland scrub dweller since it extends to pine and rainforest up to 1,700 m. In the Sierra de Baoruco these two species are broadly sympatric over a range of 1,265 m, each inhabiting scrub, rainforest, and pine forest from low foothills to high mountains. In the eastern Dominican Republic (Samaná Peninsula and San Lorenzo Bay) both occur in mangroves and lowland rainforest.

Additional indirect evidence for the Broad-billed and Narrow-billed Todies having evolved on separate islands may be found in the presence and distribution of two other species pairs on Hispaniola, viz., the Palm Tanagers (*Phoenicophilus*) and, to a lesser extent, the Ground Warblers (*Microligea*).

MULTICOLOR → *TODUS*

Plumage and morphology.—The most obvious link between *multicolor* and *todus* is the presence of the blue-gray subauriculars in *todus* which must have been derived from the sky blue cheek patch of *multicolor*, and which are represented by only a few pale gray feathers in the remaining species. The bill widths and body lengths are virtually identical.

Behavior.—The amount of Wing-flicking in both species is moderate. It is much less common than in the Hispaniolan species and more so than in *T. mexicanus*.

TODUS → *MEXICANUS*

As mentioned earlier, the origin of the Puerto Rican species from Jamaican stock is not what one would have predicted on a geographical basis. But chance is an important factor in the colonization of islands, as pointed out by Lack (1970).

These two todies are differentiated from the remaining species mainly by vocalizations, territorial and feeding behavior, and by considerably less (if any) pink flank coloration and greenish wash on the breast (only in juveniles of *mexicanus*). Similarities include the following features.

Plumage.—The small patch of pink on the flanks of the *todus* is represented by very occasional orange feathers in *mexicanus* (3 of 104 males in USMN). The yellow-green undertail coverts, belly, and flanks of *todus* are replaced by a deeper yellow in *mexicanus*. All nine juvenile *mexicanus* skins studied had obvious green breast washes, as in *todus*. The blue-gray cheek patch of *todus* (most prominent in males) is present as a few pale gray feathers in *mexicanus*.

Body measurements.—The bills are virtually identical in width in the two species, and are closer in length to one another than to any other species.

Iris color.—The iris is either slate or white in *todus* (seemingly unrelated to sex) but in *mexicanus* males it is almost always slate and in the females it is whitish. This argues against the derivation of *mexicanus* from Hispaniolan stock, as each of the two species occuring there seems to have different colored irides.

Behavior.—The Flank Displays of *todus* are the least spectacular in the family, and virtually nonexistent in *mexicanus.* Both *todus* and *mexicanus* Air-feed more than do the other species.

Vocalizations.—The typical Loud Beep and contact notes of *todus* and *mexicanus* are almost indistinguishable and are far more alike in nasal quality and duration than are the vocalizations of the remaining species. (Fig. 3.1). Throat-rattling, well–developed in *todus,* has its nearest counterpart in the seldom heard Guttural Feeding Call of *mexicanus.*

It is possible that the Cuban Tody (*multicolor*) gave rise to the Puerto Rican Tody (*mexicanus*) by a direct route, rather than via Jamaica, as these species share a yellow-orange forehead (more pronounced in *multicolor*) and also the Bobbing behavior, both characters that are absent from other *Todus.* It is also possible that the Jamaican Tody (*todus*) first landed and evolved on Hispaniola, was displaced by competition by one or two other evolving species of todies, and was blown eastward to Puerto Rico to evolve further there. However, I feel that the many important differences already mentioned between these species suggest that the route to Puerto Rico through Jamaica is more feasible.

Discussion

Todies, although superficially a uniform group, possess many behavioral, morphological, and ecological differences. Bond (1956) believed, although he did not present his reasoning, that *subulatus* was most clearly related to *todus,* and *mexicanus* and *angustirostris* to *multicolor.* However, evidence presented above seems to indicate the closest relationships are between *multicolor, subulatus,* and *angustirostris;* and between *todus* and *mexicanus.*

APPENDIX

1. STUDY AREAS OUTSIDE PUERTO RICO

HABITAT	JAMAICA	DOMINICAN REPUBLIC	HAITI	CUBA
MONTANE RAINFOREST	Blue Mountains: Cinchona to Morse's Gap (1600m-1700m) Catherine's Peak and Woodcutter's Gap (1400-1600m) Hardwar Gap area (1200-1230m) Blue Mt. Peak Trail (1400-1800m) John Crow Mountains: Road above Bath to Corn Puss Gap (500-830m)	Cordillera Central: Rio Isa headwaters, above Los Cacaos (1050m) Baoruco Range (SW): Above El Aguacate (1500-1600m)		
MONTANE PINE FOREST		Baoruco Range: Above El Aguacate (1650-1750m)	Massif de la Selle: Kenscoff and Furcy (sealevel-900m)	
COFFEE PLANTATIONS	Hagley Gap (1400m)	Cordillera Central: Rio Nizao, near Valdesia (100m) Rio Nizao, near Los Cacaos (1150m)		
DRY LIMESTONE FOREST XERIC SCRUB	Portland Ridge (130m) Hellshire Hills (30m) Mona Reservoir (200m)	Valdesia (100m) Various places on southwest coast, west of Santo Domingo, including Lake Enriquillo, Azua, El Limon, Puerto Escondido, El Aguacate (40m below sealevel-170m) Near La Caleta (15m)	Coast road on west coast on way to Gonaives (sealevel)	Guantanamo Naval Base (sealevel-130m)
MESIC LIMESTONE FOREST	Ferry River (200m)			
WET LIMESTONE FOREST	Cockpit country of northwest, Barbecue Bottom road. Fern Gully (sealevel) Worthy Park (500m)			
SECOND-GROWTH, PASTURES RIPARIAN WOODLAND	Throughout	Southern portion only	Western part	

Tody densities varied according to nature of the vegetation from zero to quite common in thickly-wooded areas.

APPENDIX

2. TRAILS AND NAMED SITES IN PUERTO RICO

LUQUILLO FOREST (see map)

Tabonuco Zone: Big Tree Trail; Sabana Ridge Road; Bisley Trail; El Verde (Puerto Rico Nuclear Center Field Station), Ox Trail, Sonodora River Trail, Tower Trail, Espíritu Santo Trail, Upper Sanodora Road.

Colorado Zone: Recreation Area Trail; Espíritu Santo Trail (from east side); Baño de Oro Natural Area; El Verde, Sanodora River and Palo Hueco Trails.

Sierra Palm Zone: Mt. Britton, La Mina Falls Trails; trail from Field Station to Mt. Britton Trail.

Elfin Forest: El Yunque and East Peak Trails; El Yunque Peak Road to junction with Mt. Britton Trail.

Ridges: El Toro and Las Cotorras Trails; Loop Roads (off Route 191); El Yunque Peak Road.

In addition, the major road across the mountain, Route 191, was checked along most of its length within the forest, passing through all zones.

GUÁNICA FOREST

East, West, North, Tamarindo, Ballena, Main, Dynamite, and Mahogany Vale Roads.

SUSUA FOREST

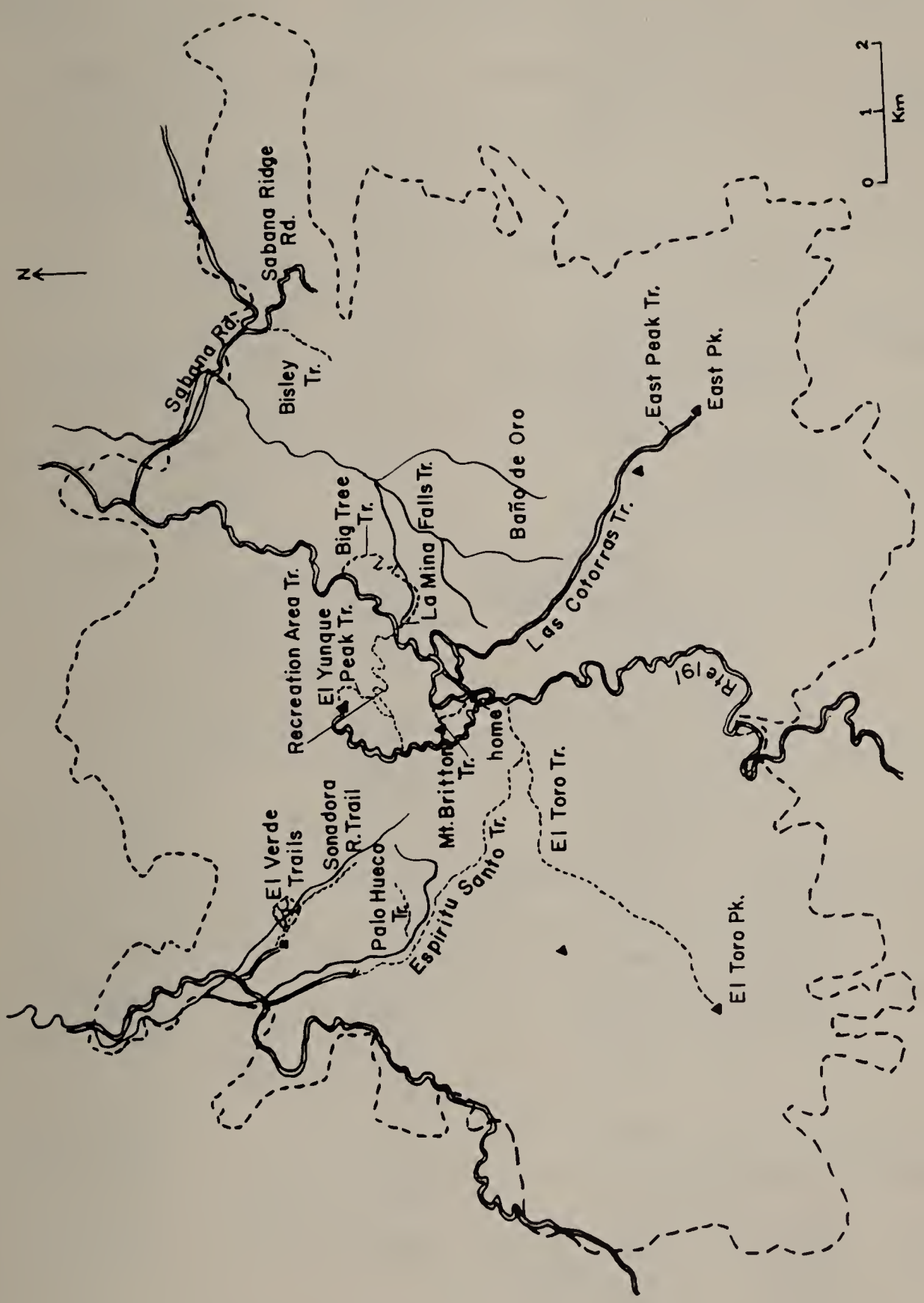
High and Low Roads (across river from Ranger's Office); Cross-Peces and Hi-wire Trails (reached by single jeep track from access road overlooking recreation area).

COFFEE PLANTATIONS

Behind Mennonite Mission, off Route 723, Cordillera Central; several plantations near Cidra.

KARST COUNTRY

Río Abajo Forest, several trails and roads; Guajataca Forest, Brecha number 1; access road beyond entrance to forest.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Sabana Ridge Rd.
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La Mina Falls Tr.
Baño de Oro
East Peak Tr.
East Pk.
Las Cotorras Tr.
Río Icacos
Recreation Area Tr.
El Yunque Peak Tr.
El Verde Trails
Sonadora R. Trail
Palo Hueco Tr.
Espíritu Santo Tr.
Mt. Britton Tr.
home
El Toro Tr.
El Toro Pk.
0 1 2 Km
LUQUILLO FOREST

APPENDIX

3. FOOD EATEN BY TODIES

ORDER	FAMILY	SPECIES	COMMENTS	REFERENCE
COLLEMBOLA (?)			Two possibly brought to nestlings	This study
EPHEMEROPTERA			Many emerging from water at dusk, taken by adults air-feeding	Danforth (1931) This study
ODONATA	COENAGRIONIDAE (damsel-flies)	*Enallagma coecum* (?)	4 and 5cm; seen once in *T. angustirostris* and *T. mexicanus*; gave todies difficulty	C. Kepler
ORTHOPTERA	GRYLLIDAE (cave-crickets, palmhoppers)	*Amphicausta grandis*, *A. caribbea*, undescribed Agraecine palmhopper	Given to nestlings and fledglings; eaten by *Eleutherodacylus coqui* and *E. portoricensis*	This study Drewry and Lavigne (unpub.)
	TETTIGONIDAE (long-horned grasshoppers, crickets)		*T. mexicanus* takes both nymphs and adults	
		Several unidentified species from either or both of these families	Adults; given to nestlings and to fledglings; difficult to identify in field to family level; nymphs of one family resemble adults of other	This study
	ACRIDIDAE (typical grasshoppers)	Several species, green and brown	Adults; given to nestlings, especially after 6th day, and to fledglings	This study
		"locust"	Stomach sample	Wetmore (1916)
	PHASMIDAE (stick insects)	Small brown and green species up to 4cm	Adults; given to nestlings	This study
	MANTIDAE (praying mantis)	*Plectoptera* sp "mantis"	Stomach sample Stomach sample	Wetmore (1916) Wetmore (1916)
DICTYOPTERA	BLATTIDAE (cockroaches)	*Cariblatta* sp	Formed 2.5% of nestling diet, mostly after 6th day; given to juveniles; also eaten by *Anolis gundlachi* and *A. evermanni*	This study Drewry and Lavigne (unpub.)
		"roach"	Stomach sample	Wetmore (1916)
DERMAPTERA	(earwigs)		9.4% of total samples; 49 of 89 stomachs	Wetmore (1916)
COLEOPTRA	HYDROPHILIDAE (water-scavenger beetles)	*Hydrochus pallipes* *Berosus interstitialis* *B. guadaloupensis* (?) *Microrhagus*	Usually found near water; stomach sample	Wetmore (1916)
	HISTERIDAE		Possible nestling food	This study

APPENDIX

ORDER	FAMILY	SPECIES	COMMENTS	REFERENCE
COLEOPTRA (continued)	SCARABAEIDAE (dung or lamellicorn beetles)	*Ataenius gracilis*	Small, near water, found in stomach sample; eaten by *A. evermanni*	Wetmore (1916) Wolcott (1948)
	ELATERIDAE (click beetles)		Nestling food, seen once	This study
	CANTHARIDAE (leather-winged beetles)	*Tylocerus* sp	Stomach sample	Wetmore (1916).
	OSTOMIDAE (bark-gnawing beetles)	*Tenebroides* sp	Stomach sample	Wetmore (1916)
	CRYPTOPHAGIDAE	*Loberus* sp	Stomach sample; also eaten by *Anolis stratulas* and *A. evermanni*	Wetmore (1916) Wolcott (1948)
	ANOBIIDAE (drug-store beetles)	*Catorama* sp	Xeric scrub; stomach sample	Wetmore (1916)
	NITIDULIDAE (sap-feeding beetles)		Nestling food; may be commonly used	This study
	COCCINELLIDAE (lady bugs)	*Cycloneda sanguinea (limbifer)* *Scymnus roseicollis* *Scymnus* sp	Stomach sample; also eaten by *Anolis gundlachi* and other lizards; Lesser Antillean Pewee, vireos; comprised 4.9% of stomach contents (Wetmore)	Wetmore (1916) Wolcott (1948)
	CERAMBYCIDAE	*Eburia quadrimaculata* *Leptuges* sp *Leptostylus* sp	Eaten by flycatchers, Adelaide's Warbler, vireos; stomach sample; eaten by *Anolis cristatellus*	Wetmore (1916)
	CHRYSOMELIDAE (leaf and flea beetles, diabroticas)	*Cryptocephalus pusio* and species *Diabrotica graminea* and species *Haltica jamaicensis* *Glyptina* sp *Cerotoma* sp *Lema* sp	Eaten by other warblers, vireos, flycatchers and all aboreal anoles; species formed 8.6% of stomach contents (not eaten by lizards, vireos, etc.) also eaten by Adelaide's Warbler, *A. cristellus* and Lesser Antillean Pewee	Wetmore (1916) Wolcott (1948)
		(?) *Physimerus* sp		
		Several species	Adults and nestlings	This study
		"Chrysomelid beetle"	Adult stomach of *T. subulatus*	Danforth (1929)

APPENDIX

ORDER	FAMILY	SPECIES	COMMENTS	REFERENCE
COLEOPTERA (continued)	PLATYPODIDAE (engraver beetles, wide-headed ambrosia beetles)	*Platypus* sp	Stomach sample; eaten by Lesser Antillean Pewee, Parula Warbler, *Anolis evermanni*, *A. stratulus*, and *A. gundlachi* in quantity	Wetmore (1916) Wolcott (1948)
	CURCULIONIDAE	*Calandra (Sitophilus) oryzae* "rice weevil"	Formed 6.5% of stomach sample; eaten by Puerto Rican Flycatcher; important part of Adelaide's Warbler diet	Wetmore (1916) Wetmore (1927)
	PLATYSTOMIDAE (fungus weevils)			Wetmore (1916)
		"beetles"	In stomachs of all species of *Todus*	Danforth (1929) Danforth (1931) Danforth (1935) Gosse (1847)
HEMIPTERA	CYDNIDAE (negro bugs)	*Amnestes* (?)	Similar to small black Coleopterans, especially Nitidulidae; either these or the beetles are commonly given to nestlings	This study
	PENTATOMIDAE (stink bugs)			Wetmore (1916)
	PHYMATIDAE (ambush bugs)	*Macrocephalus* sp	Stomach contents; common on coffee shade trees, especially *Inga* spp; resemble twig hairs	Wetmore (1916) Wolcott (1948)
		Phymata marginata (erosa)	Stomach contents; common in rainforest; eaten by vireos, warblers; usually on flowers	Wolcott (1948)
	NABIDAE (damsel bugs)		Few given to nestlings after 6th day; over 3cm	This study
		"Coreid bug"	Stomach of *T. subulatus*	Danforth (1929)
	COCCIDAE (scale insects)	*Lecanium* sp	Stomach contents; also eaten by *Eleutherodactylus portoricensis*	Wetmore (1916) Drewry and Lavigne (unpub.)
	LYGAEIDAE (chinch bugs)	*Geocoris thoracicus*	Xeric scrub; tody stomach contents	Wetmore (1916)
			Other species common under leaves, rainforest	Drewry This study
HOMOPTERA	FULGORIDAE (lanternflies)		Nymphs and adults formed 30% of nestling diet; also eaten by adults and juveniles; common in West Indies	Wetmore (1916)

APPENDIX

ORDER	FAMILY	SPECIES	COMMENTS	REFERENCE
HOMOPTERA (continued)	FULGORIDAE (continued)	*Oliaris franciscanus*	Stomach contents	Wetmore (1927)
		Ormenis sp		Wetmore (1927)
		Ladella stali	Commonly given to nestlings and fledglings	
		Acanalonia vivida	Commonly given to nestlings and fledglings	This study
	CICADELLIDAE (leafhoppers)	*Cicadella* sp		Wetmore (1916)
		Sibovia coffeaphila	Seven found in stomach of one tody	Wolcott (1948)
		Several species	Often eaten by adults; given to nestlings and fledglings	This study
NEUROPTERA (lacewings)			Few given to nestlings	This study
TRICHOPTERA (caddisflies)		One species	One possible individual brought to nestling	This study
LEPIDOPTERA (moths, butterflies)			Order constituted 16.3% of nestling diet after 6th day; 5.2% of stomach contents	This study Wetmore (1916)
	HESPERIIDAE (skippers)	At least two species	Brought to nestlings	This study
	SPHINGIDEA (sphinx moths)		Large green caterpillars given to nestlings; juveniles; adult eaten by *T. multicolor*	This study
	ARCTIIDAE (tiger moths, woolly bears)	Several species, mostly white marked with black	Adults; nestlings	This study
	CTENUCHIDAE	One species	Given to nestlings	This study
	NOCTUIDAE	Several species	Commonly given to nestlings; adults and juveniles	This study
	GEOMETRIDAE (measuring worms)	Several species *Rachaospila* sp	Caterpillars and adults; adults and nestlings	This study Wetmore (1916)
DIPTERA (flies)			Formed 20.9% of stomach contents; 3% of nestling diet (figure low); 22% of *T. multicolor* samples	This study Wetmore (1916)

APPENDIX

ORDER	FAMILY	SPECIES	COMMENTS	REFERENCE
DIPTERA (continued)	TIPULIDAE (crane flies)	Several species, large and small	Adults, nestlings, also eaten by anoles; when large, may give difficulty to todies	This study Drewry and Lavigne (unpub.)
	CULICIDAE (mosquitoes)		Stomach contents	Wetmore (1916)
	SIMULIIDAE (black flies)	*Simulium* sp *Quadrivittatum* sp	Stomach contents; common in rainforest	Wetmore (1916) Wolcott (1948)
	CHIRONOMIDAE (midges)		Adults, juveniles, nestlings; often swarms over water; at least 51 species in El Verde	This study Drewry (1970)
	STRATIOMYIDAE (soldier flies)		nestling diet; also eaten by *Eleutherodactylus portoricensis*	This study Drewry and Lavigne (unpub.)
	SYRPHIDAE (flower flies)	*Eristalis* sp	Nestling diet; adult stomach contents	This study Wetmore (1916)
	DOLICHOPODIDAE (long-legged flies)	Several species *Psilopus* sp	Nestling diet; adult stomach contents; common in forests; eaten by *Anolis gundlachi*	This study Wetmore (1916) Drewry and Lavigne (unpub.)
	OTIDIDAE (picture-winged flies)	*Eutesta* sp *Tenanops* sp	Stomach contents Stomach contents	Wetmore (1916) Wetmore (1916)
HYMENOPTERA			Order comprised 4.3% of stomach contents	
	ICHNEUMONIDAE (Ichneumon wasps)	*Nyptia* sp	Stomach contents	Wetmore (1916)
	TENTHREDINIDAE (saw flies)	One species	Stomach contents	Wetmore (1916)
	FORMICIDAE (ants)	*Kapala* sp	Stomach contents; one of principal parasites of todies	Wetmore (1916)
		Solenopsis sp *S. geminata*	Common stinging ant that invades tody nests; abundant in forest; quite a few taken by adults (Wetmore); eaten by all anoles and treefrogs	Wetmore Drewry and Lavigne (unpub.)
		"winged ants"	1.4% of stomach samples	Danforth (1931)
	CHALCIDAE	*Macromischa* sp		Wetmore (1916)
		"minute hymenoptera"	Stomachs of *Titodus*	Gosse (1847) Wetmore (1916) This study

APPENDIX

ORDER AND CLASS	FAMILY	SPECIES	COMMENTS	REFERENCE
Insect Eggs			Few in stomach samples	Wetmore (1916)
ARACHNIDA Araneida (spiders)			Spiders formed 3% of nestling food; 8.2% of stomach contents	This study
		Reddish-brown, probably *Metepeira labyrinthea*	Many given to nestlings	
		Attid spider	Stomach of *subulatus*	Danforth (1929)
		Mogrus sp *Epeira* sp	Stomach contents	Wetmore (1916) Danforth (1929)
DIPLOPODA		"small millipede"	Stomach of *subulatus*	Danforth (1929)
NEMATODA (nematodes)			One given to nestlings; taken by one or two adults; eaten by *E. portoricensis* and other treefrogs	This study
REPTILIA	IGUANIDAE	*Anolis* sp	Tiny *Anolis* found in five stomachs	Wetmore (1916)
ANGIOSPERMAE	MORACEIAE	*Ficus* sp (fig)	Few seeds	Wetmore (1916)
	CHENOPODIACEAE	*Cenopodium* sp	Few seeds	Wetmore (1916)
	ROSACEAE	*Rubus* sp (raspberry)	Few seeds	Wetmore (1916)
		Xanthoxylum sp	Few seeds	Wetmore (1916)
	RUBIACEAE	One species	Few seeds	Wetmore (1916)
		Psychotria berteriana (black berries)	2 or 3 eaten by perched adult attending nest	This study
	PAPAVERACEAE	*Bocconia frutescens*	Several fruits taken in flight by *T. angustirostris* in Dominican Republic	This study
	BRUNELLIACEAE	*Brunellia comocladifolia*	One bud taken in flight by *T. todus* in Jamaica	
	?	"few seeds"	Stomachs of *T. todus*	Gosse (1847) Danforth (1931)

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